Systematic Zoology

SOCIETY OF SYSTEMATIC ZOOLOGY

MUSEUM LIBRARY

Historical Subspeciation in the North American Marten — *L. S. Dillon* — 49

The Classification of Parasitic Gastropods — *E. S. Tikasingh and Ivan Pratt* — 65

Distance as a Measure of Taxonomic Similarity — *R. R. Sokal* — 70

An International Taxonomic Register: Preliminary Proposals — *W. L. Brown, Jr.* — 80

Higher Categories and Phylogeny — *R. S. Bigelow* — 86

Current Tendencies to Increase the Number of Higher Taxonomic Units among Insects — *D. K. McE. Kevan* — 92

THE UNIVERSITY OF MICHIGAN
JUN 18 1963
MUSEUMS LIBRARY

VOLUME 10 JUNE 1961 NUMBER 2

Systematic Zoology

LIBBIE H. HYMAN, *Editor*

Editorial Board

J. C. MOORE	1961	H. H. ROSS
C. D. MICHENER	1962	G. L. VOSS
A. E. EMERSON	1963	R. PENNAK
F. PITELKA	1964	C. M. BOGERT

SYSTEMATIC ZOOLOGY is published quarterly, on or about the tenth day of March, June, September, and December, by the Society of Systematic Zoology. Manuscripts and correspondence about the contents of the journal and other editorial matters should be addressed to the editor, Dr. Libbie H. Hyman, American Museum of Natural History, New York 24, New York.

Subscription rates are $4.00 to members, $6.00 to non-members and institutions. The price of single numbers when available is $2.00. Back volumes are available at the rate of $8.00 per volume when in stock. Annual dues are $2.00. Correspondence regarding subscriptions, purchases, non-receipt and all other non-editorial business should be addressed to the Business Manager, Dr. Jay M. Savage, Department of Biology, University of Southern California, Los Angeles 7, California. Correspondence concerning membership and other aspects of the Society's affairs should be addressed to the Secretary, Dr. R. Tucker Abbott, Academy of Natural Sciences, Philadelphia 3, Pennsylvania.

The Society of Systematic Zoology

OFFICERS FOR 1961

President.....R. E. BLACKWELDER
Southern Illinois University

President-Elect.....C. S. SABROSKY
United States National Museum

Secretary.....R. TUCKER ABBOTT
Academy of Natural Sciences, Philadelphia

Treasurer.....H. H. HOBBS, JR.
University of Virginia

Business Manager.....J. M. SAVAGE
University of Southern California

Program Officer.....C. F. LYTLE
Tulane University

THE COUNCIL

R. H. BAKER	1961	R. L. USINGER
J. W. WELLS	1962	H. VAN DER SCHALIE
W. K. EMERSON	1963	E. MAYR
F. CHACE	1964	R. R. MILLER

Second Class Postage Paid at Los Angeles, California;
and additional mailing offices

Historical Subspeciation in the North American Marten

LAWRENCE S. DILLON

Introduction

RECENTLY Hagmeier (1958) published a study of various morphological traits found in the *americana* group of subspecies (Fig. 1) of the marten (*Martes americana* Turton, 1806), in which the distribution of the variations of each trait was carefully mapped. On the basis of these maps, he arrived at the conclusion that in the marten "the partitioning of the species into subspecies was completely arbitrary, because most variation was clinal and because at least some characters varied discordantly." On the basis of present day distribution, there is much to substantiate Hagmeier's position in the matter.

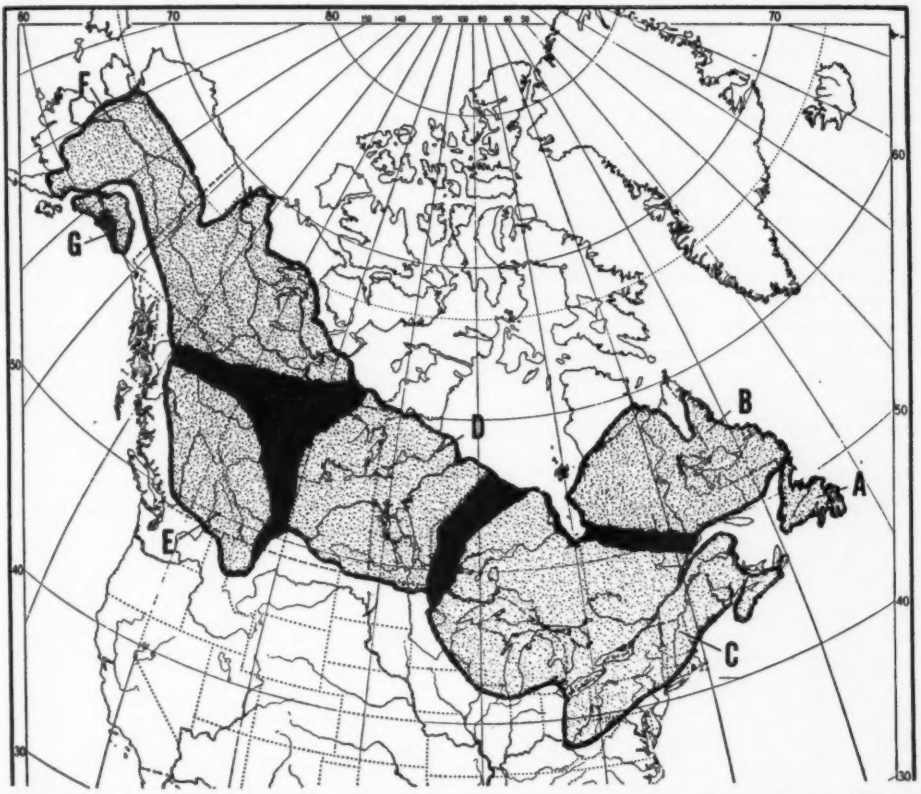

FIG. 1. The distribution of the present marten subspecies of the *americana* group according to Hagmeier (1958). Zones of intergradation are shown in black. A, *atrata;* B, *brumalis;* C, *americana;* D, *abieticola;* E, *abietinoides;* F, *actuosa;* G, *kenaiensis.*

If further thought is given to the subject, however, it may be discerned that today this mammal occupies a region which no more than 12,000 years ago was largely or entirely covered by the continental glaciation of the Wisconsin Ice Age. Hence in its present distributional patterns are included morphological variations not only that have arisen since that time but those which may have existed in earlier periods. As some additional light may be thrown upon conditions prevailing during or preceding the Wisconsin glaciation as well as upon the general topic of subspeciation itself, it was felt that a new analysis of Hagmeier's data might be beneficial, keeping in mind historical aspects in addition to contemporary ones.

Preliminary Considerations

Before reexamining the morphological data, a few aspects of the marten's characteristics may well be recalled to mind. The marten as stated by Hall and Kelson (1959) is arboreal, feeding largely on rodents, especially red squirrels (*Tamiasciurus hudsonicus* Erxleben, 1777). Further it is said to remain active all winter and to travel up to ten miles in a single night. As the population density is rather low and the territories large, gene flow between adjacent populations would be expected to be rather rapid, especially in view of the probable polygamous habits of the male (see Davis, 1939; Dalquest, 1948; Burt, 1957).

Since the marten is strictly an animal of the forest, it could not have crossed onto this continent from Eurasia during the Wisconsin, for the Alaskan-Siberian land bridge supported only tundra then and probably throughout the Pleistocene when present (Hopkins, 1959). Hence the marten has inhabited this continent since at least Pliocene times, an assumption that appears to be supported by fossil evidence (Hall, 1926, 1931) as well. Besides its arboreal leanings, another habit of the marten bears on its zoogeography, namely its distaste for swimming. Cahalane (1947) points out that it avoids entering water as far as possible, never engaging in fishing and frequently travelling long distances in search of a fallen log to avoid swimming even a small stream; however, as de Vos points out (1952), it will voluntarily take to the water on occasions. But by and large, the mammal's presence on islands at any considerable distance from the mainland may safely be assumed to have been effected through accidental transport on rafts, via former land bridges, or perhaps across ice.

Reanalysis of Condylobasal Length

Upon examining Hagmeier's study, one finds he converted his data into coefficients expressed in decimal fractions between zero and unity and that he grouped these into parcels of two-tenths each, the various parcels subsequently being mapped. Hence the maps expressed five subdivisions of each of five separate morphological features.

The fitting of these isarithms to the map were approximations only, according to Hagmeier, and hence subject to error; also for the sake of simplicity, in reanalyzing the data, the two lowest and the two highest parcels will be combined, thus reducing mapping to the expression of three subdivisions in each case. This treatment in no way alters the data but clarifies the distribution of the extreme values by eliminating confusing details. Figures 2 to 11 therefore only show the distribution of high and low coefficients plus a zone of intermediate values.

Treated in this way, the first of Hagmeier's traits, condylobasal length (Fig. 2), falls into three well-marked zones, each interrupted once. Whereas the highest values, populations X and X′, are divided narrowly by James Bay, the other two values are subdivided quite broadly in the region of the Great Plains. Or the same facts might be expressed in terms of the lowest values occurring in two widely separated populations, Z and Z′, with in-

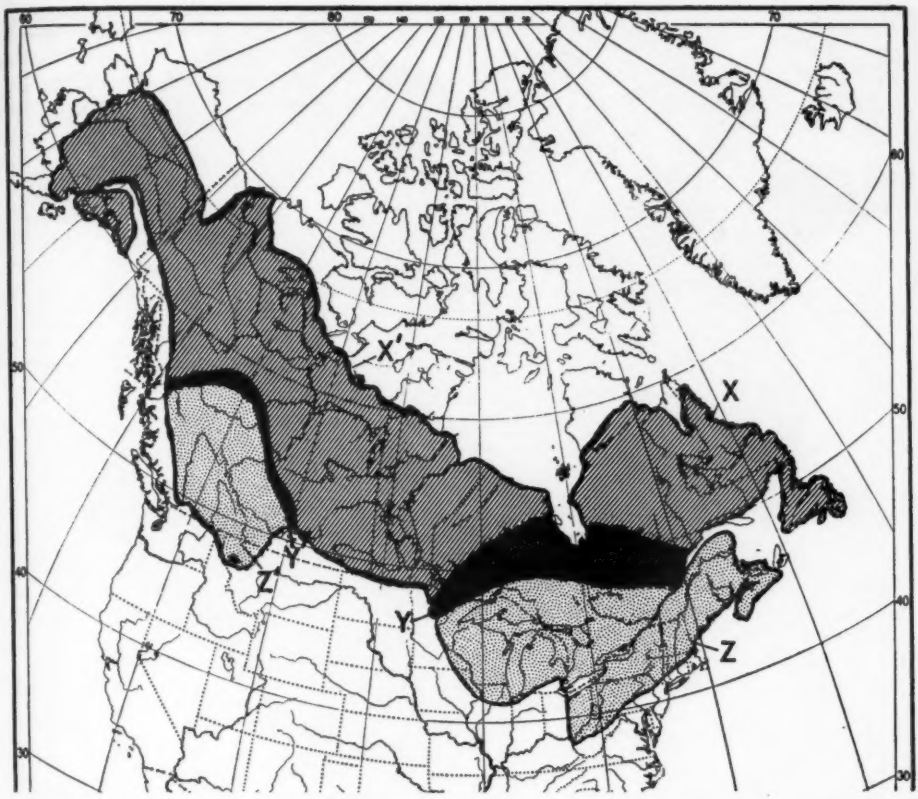

FIG. 2. Present-day distribution of condylobasal length values. The highest values (.6–1.0) are indicated by X and X', the lowest (0.–.4) by Z and Z', while the intermediate values (.4–.6) are shown in the black zone labelled Y and Y'.

termediate values, Y and Y', occurring wherever contact was made with populations X or X'. If during the Wisconsin Ice Age, the glaciation over the northern reaches of the continent produced a condensation of the life zones, as has been postulated elsewhere (Dillon, 1956), the distribution of the marten may have approximated that suggested in Figure 3. It should be clearly understood that the westward extent of distribution cannot be established beyond doubt by any existing evidence nor can the actual width of the three population bands, X, Y, and Z, be ascertained. In fact, the very existence of these populations is hypothetical, as is that of the Rocky Mountain population, Z'. Nevertheless, if the suggested pattern is accepted as plausible, two possible accounts of post-Wisconsin events can be suggested to explain the present day distribution of the condylobasal length, as follows: in the first of these, as glaciation receded subsequent to initial elevation of the temperature, the four populations, X, Y, Z, and Z', expanded their areas of occupation and moved northward. population X following the rapidly expanding spruce forests; the thicker, less rapidly melting, ice-masses of the Rocky Mountains prevented Z' from doing so. As these movements continued after further

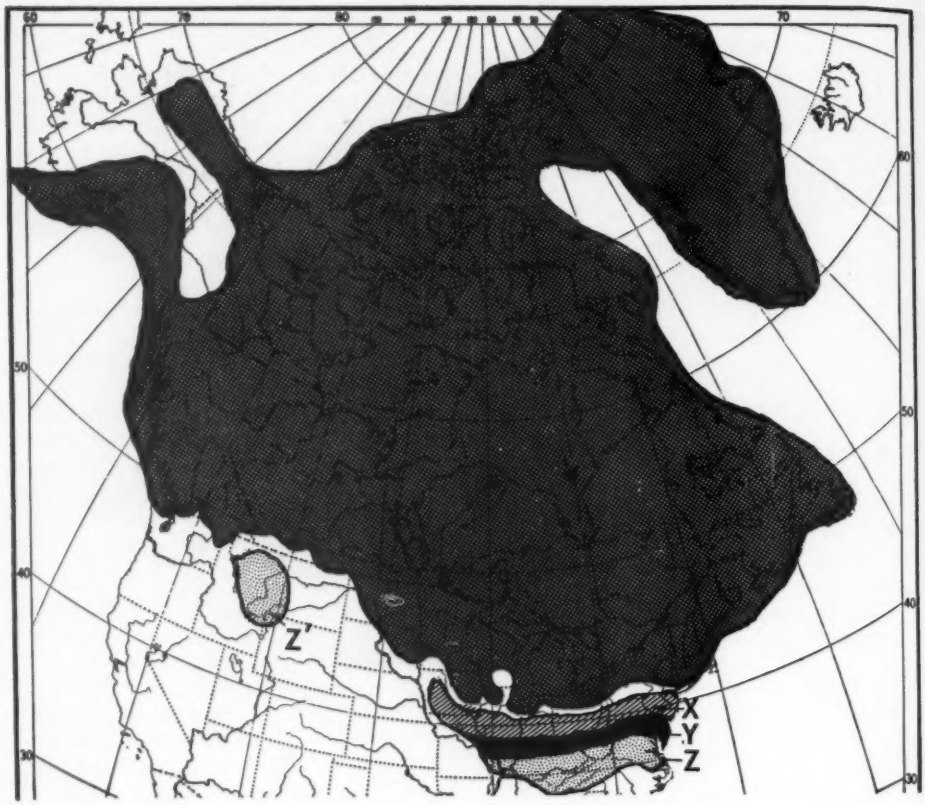

FIG. 3. Hypothetical distribution of condylobasal length values during the maximum extent of Wisconsin glaciation. The darkly hatched area represents the area under glaciation; other abbreviations as in Figure 2.

elevation of temperature and recession of the ice-sheets (Figs. 4 and 5), population X, in the north, gradually became bisected by the southern extension of the Hudson Bay (James Bay), while in the west a new intermediate population, Y', eventually sprang up where population X came into contact with Z' (line C on Fig. 5). Further migrations with the gradual disappearance of glaciation then would result in time in the present distribution of these populations as shown in Figure 2.

In the second explanation of the distribution of the condylobasal trait, historical events would be essentially the same as in the first, but the assumption would be made that population Z' of Figure 3 was non-existent; in every other feature the suggested distribution at Wisconsin maximum would be identical, as would the post-Wisconsin history also. However, it would be suggested in addition that, after the populations under consideration had attained virtually their present positions, the additional increase in temperature of the hypsithermal stage enabled population Z to extend westward (Fig. 6) and to occupy this area of the

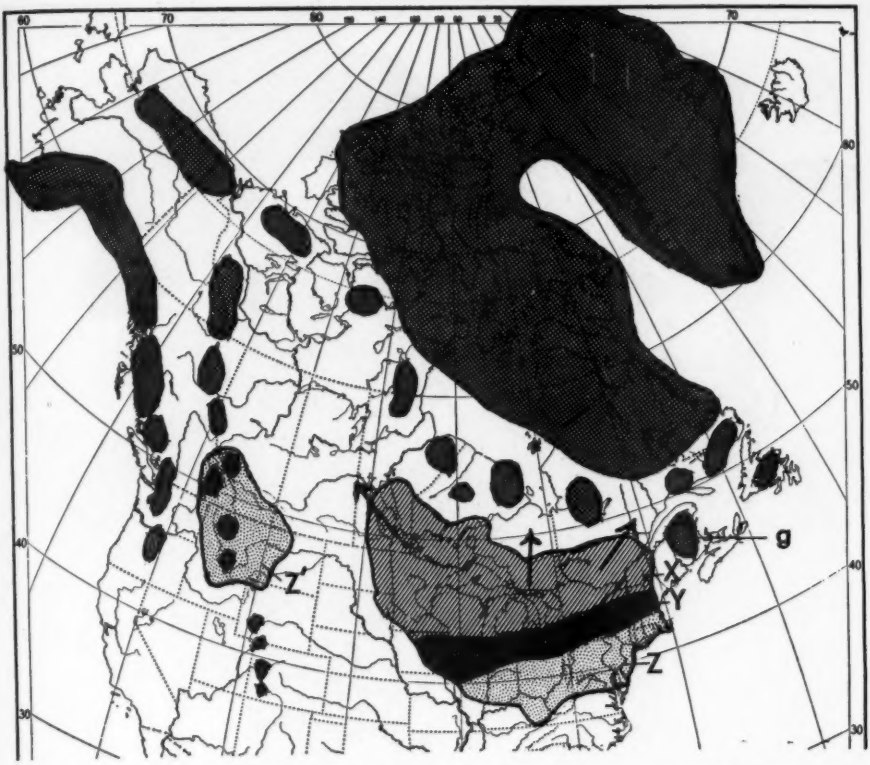

FIG. 4. Hypothetical distribution of condylobasal values after reduction of the glaciation had commenced; as the forests spread into areas recently freed of ice, the martens follow. g, glaciation or some persistent barrier to the Nova Scotian peninsula; other abbreviations as in Figure 2.

Rocky Mountain region, so that Z and Z′ would be subdivisions of one and the same population.

In both hypotheses, it is necessary to assume the presence of some restricting factor in the east which prevented X and Y from entering Nova Scotia. Whether the blockage of this area was due to persistent glaciation athwart New Brunswick as indicated in Figures 4 and 5 or to the submergence of the land below sea level or to some other factor is irrelevant; the point is that some sort of barrier seems effectively to have prevented the more northern populations from inhabiting these maritime provinces. Without a barrier it becomes extremely difficult to understand why New Brunswick, Nova Scotia, and the adjacent islands are consistently occupied by the southernmost population, without a single clear trace of the northern one which otherwise would have arrived first.

Canine Width

In like manner it is possible to explain the present-day distribution of several of the other morphological traits in terms of its Wisconsin and post-Wisconsin history. In each instance the Wisconsin distribution is assumed to have been comparable

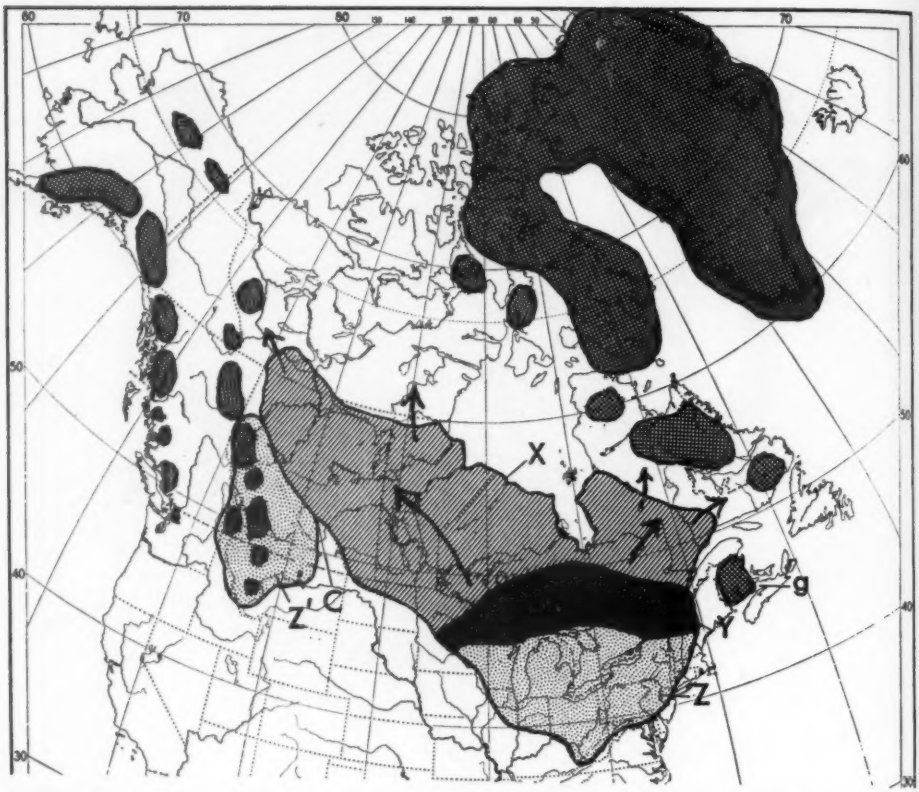

FIG. 5. Hypothetical distribution of condylobasal length values upon further reduction in glaciation. C, line of contact between populations X and Z′ where hybridization might occur; g, glacier or other barrier to the Nova Scotian peninsula; other abbreviations as in Figure 2.

to that suggested for condylobasal length (Fig. 3), with subsequent events identical for all, with minor variations. Canine width in its simplified arrangement (Fig. 7) shows a similar distribution pattern today as that of condylobasal length, except that the intermediate population is broken into a number of segments. These segments may have been interconnected at one time to form a single continuous zone of intergradation as suggested in Figure 8. Subsequent shifts in populations have formed deep folds in the zone, which eventually resulted in partitioning into the segments. This folding and deformation in this trait and its absence in the first is understandable if it is noted that the zone of highest values, X and X′, is much narrower than in condylobasal length and the intermediate zone much broader and more extensive with the lowest values slightly so. Hence the three zones of the two characters would not have been precisely co-extensive during Wisconsin times; only a relatively small percentage of martens with high condylobasal values would have also possessed high canine width ratios, probably the most northern members of the zone. A large percentage of the population with

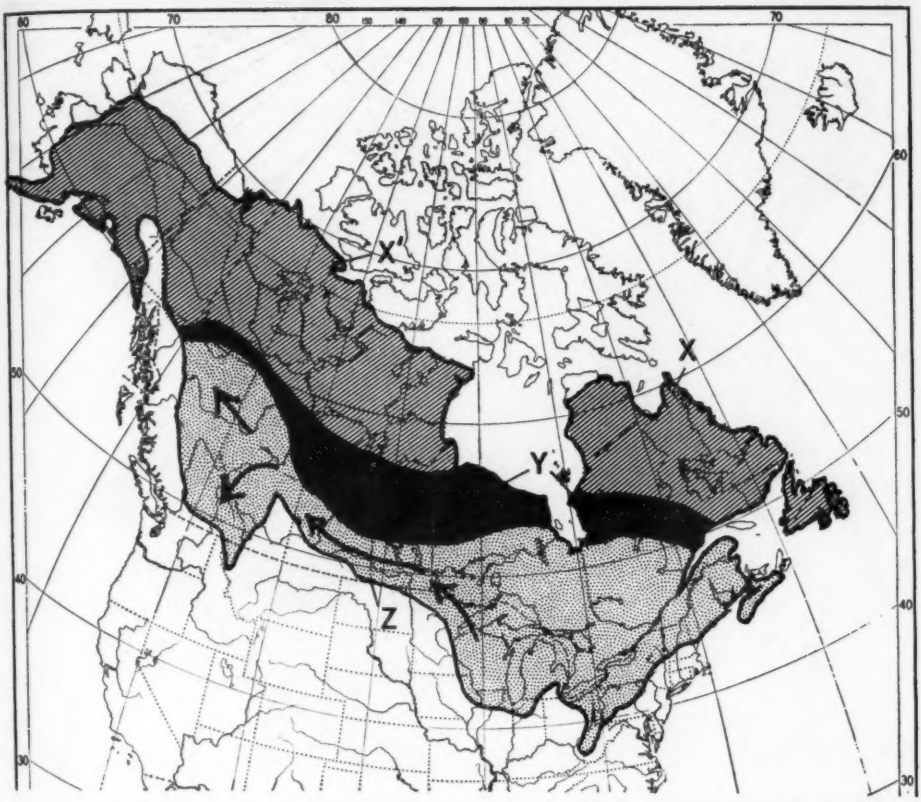

FIG. 6. Alternative hypothetical distribution of condylobasal length, possibly occurring during the hypsithermal post-Wisconsin stage. If a sufficient rise in temperature occurred, population Z could have reached the Rocky Mountain area, eliminating the necessity of hypothesizing the presence of a separate Z′ population during and following the Wisconsin climax. Population designations as in Figure 2.

high condylobasal values, those occurring slightly farther south, would have possessed intermediate canine widths.

As in condylobasal length two origins of populations Z′ and Y′ can be advanced. If Z′ were separated from Z all through the period of glaciation, Y′ could represent interbreeding between X′ and Z′ since the melting of the ice-sheet. If, on the other hand, Z′ is a recent introduction following the hypsithermal post-glacial stage, Y′ is, largely at least, a fraction of the eastern Y population. In Alaska, the intermediate population Y″ could represent either independent mutation of X′ to a lower value or a possible remnant of Y′ from the hypsithermal period.

Reconsideration of Other Traits

In its simplified version, rostral width ratios seem to fall into the same general pattern (Fig. 9) as the two morphological traits already considered. The population with highest values, R and R′, appears to be more restricted than was the case with

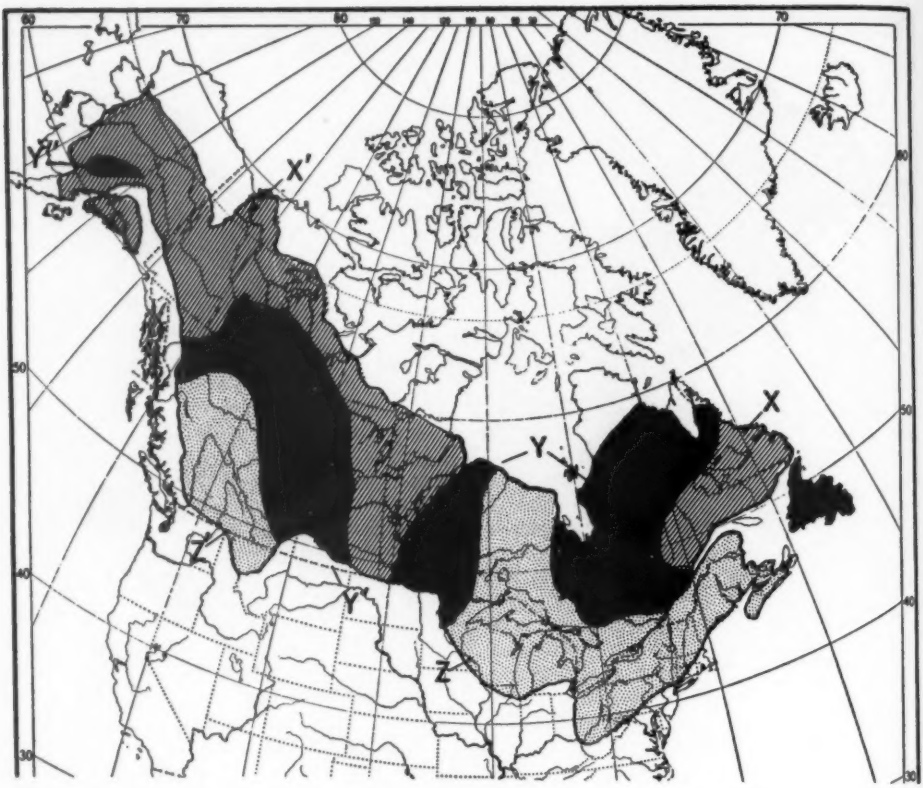

FIG. 7. Present distribution of canine width values, simplified from Hagmeier. X, X', populations with values from .6–1.0; Z, Z', populations with value range of 0.–.4; Y, Y', Y", populations of intermediate values, .4–.6.

either of the preceding characters, in the east being restricted solely to Newfoundland. Also, in the eastern portion of the marten's range, the population (T) with lowest rostral width values has migrated north of that with intermediate values (S). But otherwise the sequence of zones is clear-cut, and the present pattern of distribution can readily be derived from the Wisconsin distributional pattern suggested for condylobasal length (Fig. 3), with a similar post-Wisconsin history. However, here it would seem that the population Z' of the maps of this sequence was possibly in actuality isolated from the eastern population Z, for in the present characteristic of rostral width, it does not agree with the southern components, possessing intermediate values instead of low ones.

In view of the fact that this population in the southwestern portion of the range has agreed with the southeastern population in two traits, this disagreement in a third would not be very convincing evidence favoring disjunction between the two populations during Wisconsin maximum by itself. But when taken in conjunction with the two traits remaining for discussion, bulla length and upper molar

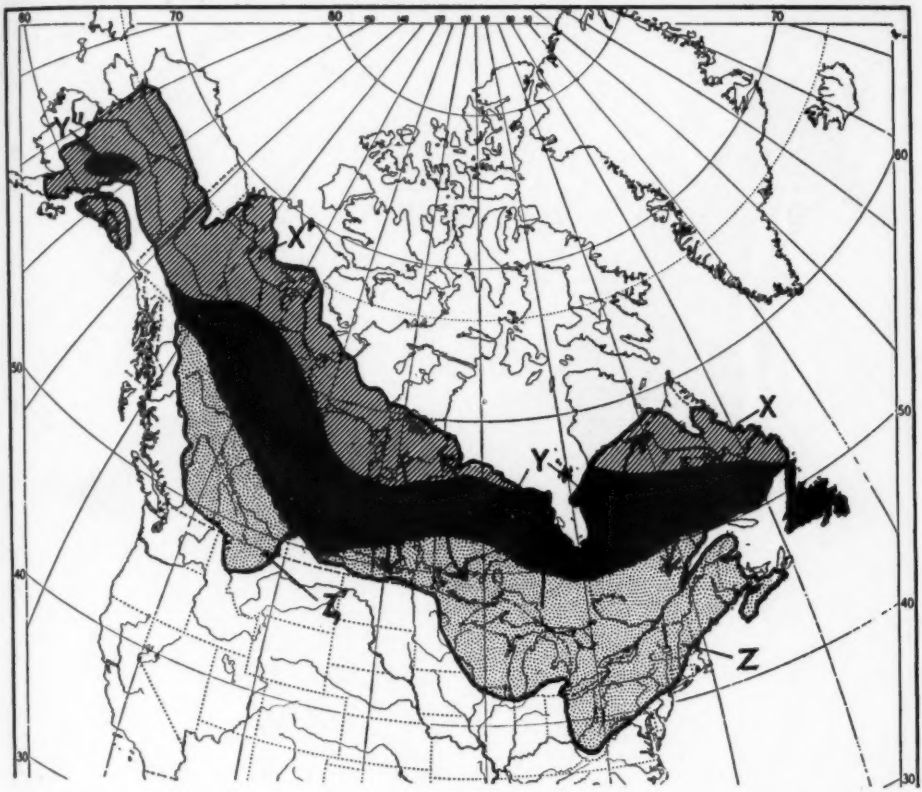

FIG. 8. Suggested former distribution of canine width values, showing the intermediate populations as a continuous zone which later became folded as in Figure 7 through random migrations of members of the several populations. Y', a segment which could have arisen independently through interbreeding of X' and Z'.

length, these two populations appear to be quite distinct, reflecting long isolation from one another. But more will be said of this matter later when the various subspecies are compared; at the present time it is more pertinent to discuss the other details of distribution of the remaining two traits. In the map showing the geographic relations of bulla length ratios (Fig. 10), it is to be noted that the highest values of this character are confined to the southwestern population, as most of the martens throughout the range are of the lowest values. Exceptions to this statement are confined to the extreme eastern and northwestern portions of the range, in addition to the zone of contact (O') between the extreme types. Since the southwestern population (N) appears to have been isolated during the glacial maximum, this zone of contact probably would have arisen by interbreeding since deglaciation occurred. Populations O and O" could represent, contrariwise, remnants of a previously existing population confined to the northern margin of the marten-occupied area during the Wisconsin; the only visible alternative is that of independent origin in each of the three areas. If the former is actually the case,

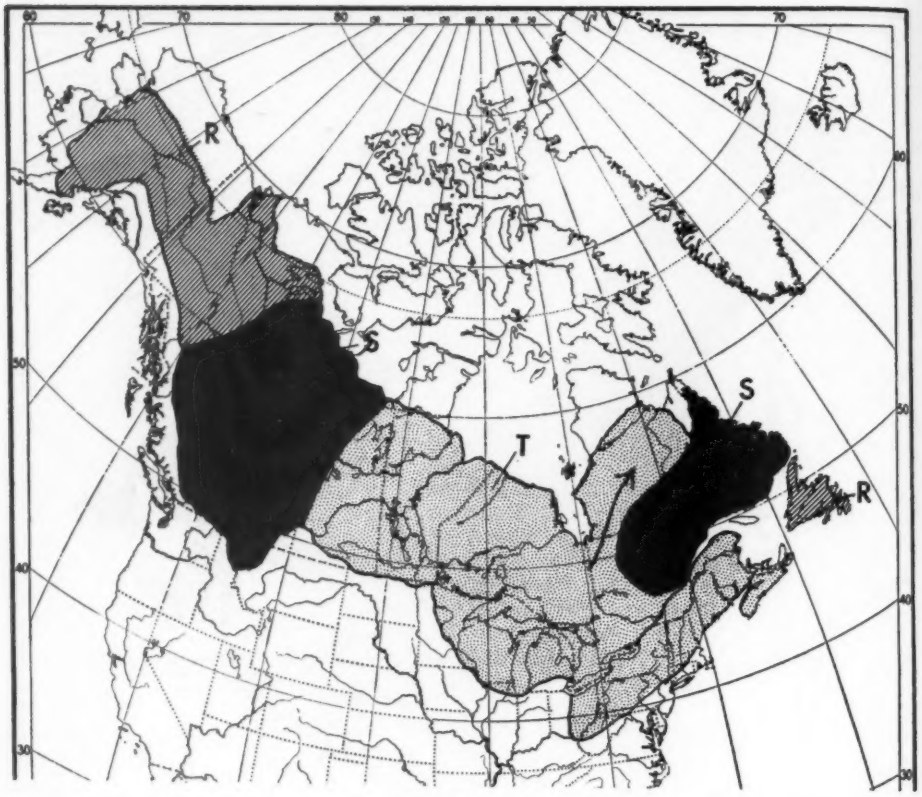

FIG. 9. Present distribution of rostral width values. R, R′, populations with highest value range .6–1.0; S, S′, intermediate populations, with range .4–.6; T, population with lowest values, 0.–.4.

this is the only instance in the traits here analyzed where a trace exists in New Brunswick and Nova Scotia of such northern elements. Further, it will be noted that a low bulla length value is, as a whole, a remarkably constant feature of the *americana* group of subspecies.

In the last of the five structural features discussed by Hagmeier, upper molar length, there also is extensive uniformity throughout much of the area; the majority of the species possess an intermediate value in this case (Fig. 11). Here the reverse of the usual situation prevails; the most northern populations appear to have possessed the lowest values, rather than the highest as heretofore. The subdivisions of this trait-value zone (L and L′) are confined to Newfoundland and the far west, whereas Hagmeier's map giving the finer subdivisions indicates that the very lowest values (0–.2) are confined to Newfoundland and to southern Alaska. Hence much of the area labelled L′ in Figure 11 could be looked upon as being intermediate between these lowest extremes and the middle values (K, K′ and K″). His map, too, shows that J′ is not so extreme as the southwestern population J, for the latter has an actual isarithm

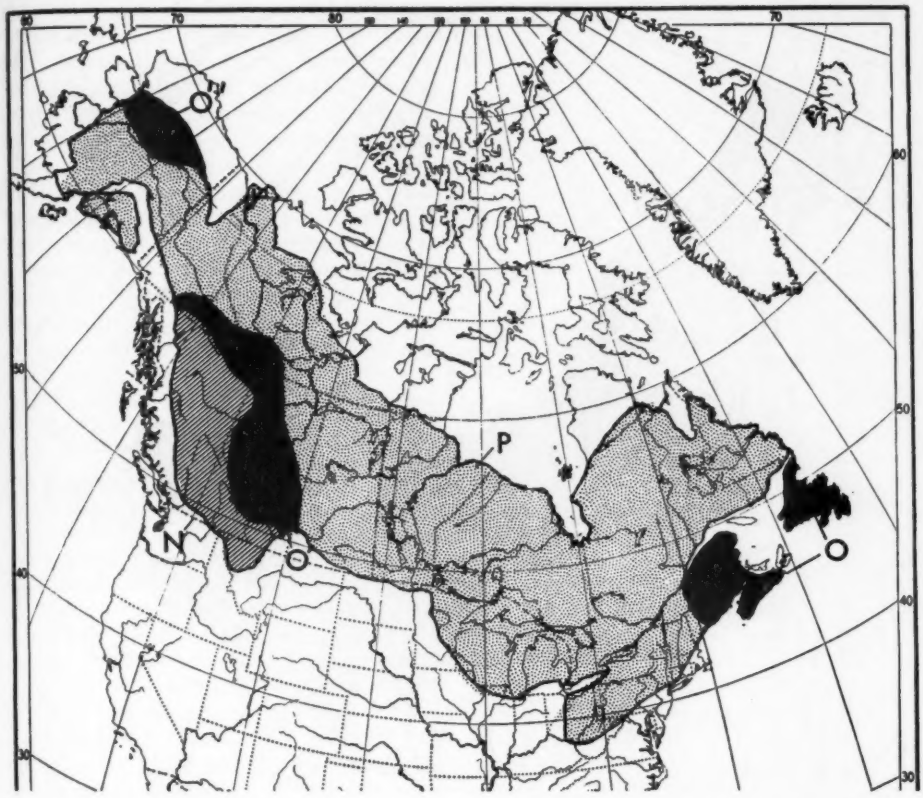

FIG. 10. Present distribution of bulla length values. N, sole zone of highest values, .6–1.0; O, O′, O″, zones of intermediate values, .4–.6; P, extensive zone of lowest values, 0.–.4.

value of .8 to 1, whereas the former lies in the range of .6 to .8. J′ then might well be looked upon as being of independent origin, a population difference that has arisen spontaneously since deglaciation. While K″ seems to represent a segment formerly continuous with K, K′ could have come into existence by interbreeding between populations J and L′.

None of the five traits reexamined here are discordant with the proposals that during the Wisconsin glaciation the martens of the *americana* group of subspecies occupied two portions of the present United States, one confined to the Rocky Mountain area, the other to the northeastern unglaciated region, and that the latter group was stratified at that time in regard to these morphological characteristics. Further in all cases the present distribution of traits can largely be explained on such an historical basis.

The Subspecies Question

Hagmeier rejected the subspecies concept as far as this group of marten varieties is concerned because he found that only one of the five traits which varied geographically coincided even approximately with the distribution of the generally accepted subspecies of marten. But is

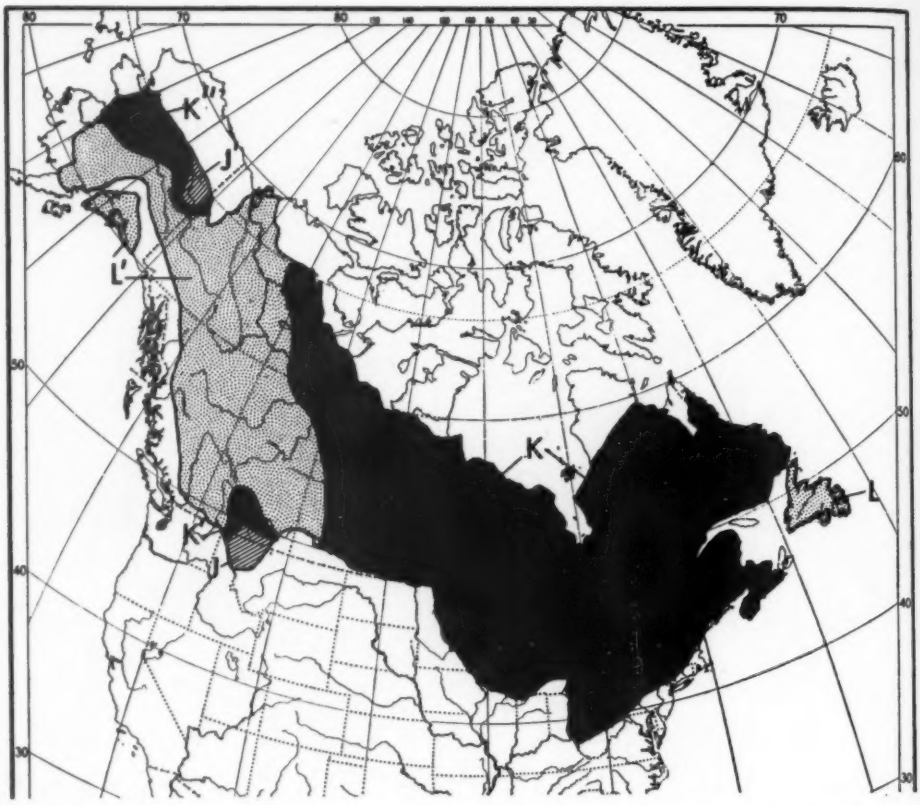

FIG. 11. Present distribution of upper molar length values. J, zone of highest values, .8–1.0; J′, zone of next highest values, .6–.8; K, K′, K″, populations with intermediate values, .4–.6; L, L′, populations with lowest values, 0.–.4.

this a valid basis for rejection of the concept? Is it reasonable to demand that a whole constellation of geographically varying characteristics coincide in their distributional patterns in order that the populations under question be considered of valid subspecific rank? For the latter condition to arise, would it not be necessary for all the genetical mutations to have occurred simultaneously, if gene flow is at a uniform rate in each case? And not alone would it be essential for each gene change to have occurred simultaneously but also that each arose in approximately the same area, so that the spread across the entire range of the organism, north and south as well as east and west, would, in every case, proceed uniformly. Is this not demanding much of chance alterations in genetical makeup?

Since mutations obviously do not necessarily occur simultaneously nor at the proper localities, it is not requisite that all show the same approximate boundaries when mapped; it is only required, in the present writer's opinion, that the variations between populations be real (i.e., show measurable range-differences) and that these be correlated with geography or, in some cases, with ecology. While in

practice a single measurable trait, within a major segment of the species and properly correlated as stated above, would validate application of subspecific names to the respective populations, in most instances many more differences would become evident upon closer study. Hagmeier's very thorough, careful work upon the subspecies of marten has brought to light many more distinctions between the various adjacent populations than were previously suspected. These differences between adjacent and widely separated populations are here summarized in Table I.

Examination of this table shows that the Newfoundland population (A in Fig. 1) is 80% distinct from that (B) occupying the neighboring mainland belt. From the latter it is constantly distinct in relative width of the rostrum and length of the upper molar and the bulla, in addition differing from a large portion of B in condylobasal length and canine width. Would it be justifiable then to imply that this population is not distinct from the mainland form by declining to recognize it as a valid subspecies? In the same manner population B is seen to differ in about half of the traits under consideration from the southeastern population C. Under such circumstances would it not be equally arbitrary not to recognize the two populations taxonomically as to do so?

A comparison of populations B and D shows entirely different results, however. These two agree in every detail except in the matter of rostral width, in which some degree of difference prevails between large portions of them. Therefore it is clear that B and D are actually only segments of one and the same population which have become separated from one another only in fairly recent years, so that genetic differences have not as yet had opportunity to accumulate. This relationship of B and D is corroborated by a comparison of the latter with the southeastern population. On making the comparison it becomes evident that C differs

TABLE I.—COMPARISON OF POPULATIONS BASED ON HAGMEIER'S ORIGINAL MAPS.

Trait	Populations Being Compared										
	A—B	B—C D—C	B—D	B—F D—F	C—F	C—A	A—F	E—D	E—F	E—C	F—G
Condylobasal length	+	+	0	0	+	+	+	+	+	0	0
Canine width	+	+	0		+	+	+	+	+	0	+
Rostral width	+	+	0	+	+	+	0	+	+	+	+
Upper molar length	+	0	0	+	+	+	+	+	+	+	+
Bulla length	+	+	+	+	+	+	+	+	+	+	0
Difference	80%	50%	10%	50%	80%	80%	40%	100%	90%	60%	30%

0 indicates no difference between the populations being compared, + indicates differences between approximately half of one population being compared and the whole of the other, while + + marks those cases where the two populations are totally distinct. Thus a total of ten plus-marks is possible for the sum of the five traits. The actual number of plus-marks divided by the ten possible and the result multiplied by 100 gives an estimate of the degree of differences between populations in regards to these five traits, expressed as percentages.

from D in exactly the same characters and in degree of difference as C differs from B. Similarly comparisons of D with its neighboring population F, as well as of B with the same population, show distinctions in about half of the traits, an indication of the virtual identity again of B and D and the distinctiveness of the northwestern population. Upon comparison of the Alaskan population, F, with the southernmost population, C, marked contrasts become apparent; differences in all traits exist to the extent of 80%. A similar degree of difference is demonstrated when the Newfoundland population (A) is compared to the southeastern C; however, when the two extremes A and F are examined against one another, only partial differences are found. In the latter case, it becomes evident that A and F were at one time probably parts of the same population but have been isolated sufficiently long to have established some degree of difference between them, although these differences are never sharp.

Comparisons of the southwestern population (E) against its neighboring and other segments are of especial interest. With its neighbor to the east (D), it shows differences of 100%, while with that to the north (F), distinctions to the extent of 90% are apparent. When this segment is compared with the southeastern population, a 60% difference can be noted. From these facts it may be inferred that E has no close affinities with its immediate neighbors either to the east or north, but is most closely allied to the southeastern segment of the species. However, from the latter it is so distinct that the two appear to have been isolated from one another for some time, probably at least since the Sangamon Interglacial.

Finally, comparison of the small Alaskan population G with that occupying most of the region (F) shows that the two are distinct only in part, to the extent of about 30%. Hence it may be seen that comparisons between marten populations of morphological traits which vary in correlation with geography bring out differences ranging from 10 to 100%. With these distinctions established, the question next arises as to where to draw the line between "valid" and "invalid" subspecies; the use of the quotation marks implies that opinion must be involved here. Since only three of the 13 comparisons drawn result in figures of less than a 50% difference, this degree of difference might be more generally acceptable as the criterion in the marten (Mayr, Linsley, and Usinger, 1953). On this basis (see Fig. 12) the populations C (*americana*) and E (*abietinoides*) would rank as valid subspecies as at present, while B (*brumalis*) and D (*abieticola*) could be joined into one under the name of *brumalis*, and F (*actuosa*) would be combined with G (*kenaiensis*) to form more realistic subspecies. On a strict basis these latter two populations, F and G, would have to be combined with the Newfoundland population A, for the former differ from the latter only to the extent of 40%. However, some mammalogists would probably feel that the thousands of miles intervening between A and F-G would justify application of distinguishing names to the two.

Clinal and Subspecific Characters

Since many of the traits Hagmeier studied show clinal trends, the question might be raised as to the acceptability of these in distinguishing populations (Huxley, 1939). To answer this, another question must first be raised: why are some characters sharply delimited while others are clinally distributed? What fundamental differences are there between the two that one type should be available in delimiting subspecies while the other should not? One must turn to simple genetics to receive the answers.

A little thought devoted to the questions (Sibley, 1954) brings to light the fact that probably those genetical mutants which show simple dominance will result in sharply defined phenotypic differences.

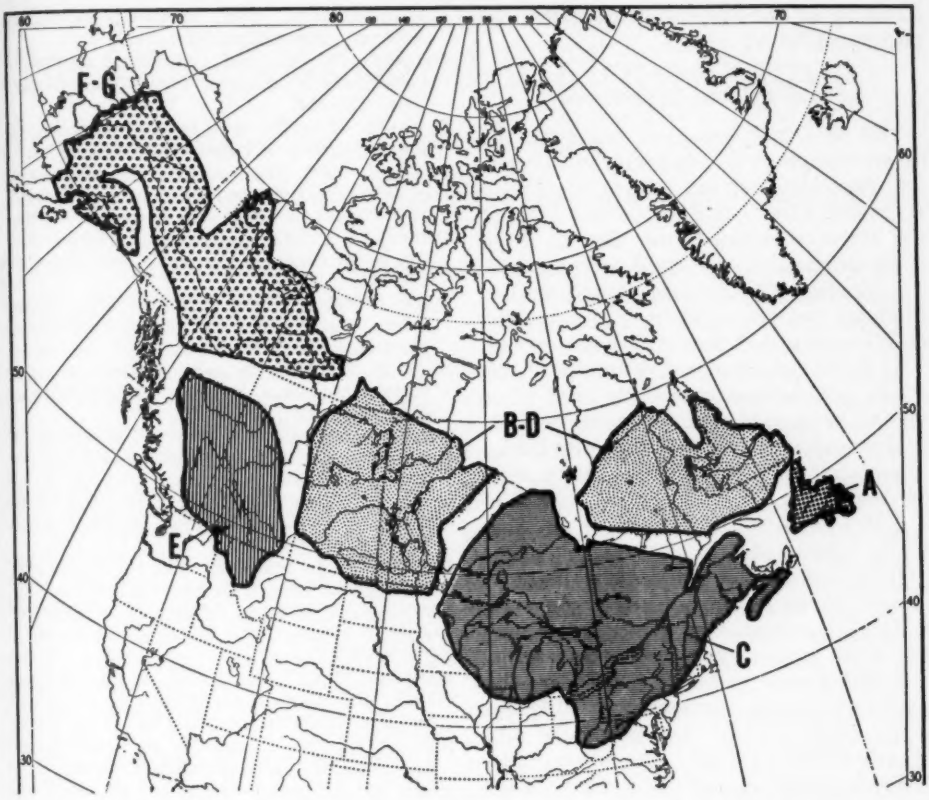

FIG. 12. The suggested valid subspecies B and D are suggested as being segments of the same subspecies, F and G are combined, while C and E are each found to be distinct; A may be treated either as doubtfully distinct or as indistinguishable from F-G.

As a hypothetical example, pigmented individuals can always be distinguished from albinos. No intermediates occur, because either the individual is capable of forming pigments or it is completely unable to do so. In a case of this sort, sharply marked populations could arise. On the other hand if a *blending* effect results in the heterozygous condition and in cases where a large number of allelic sets of genes are involved, will not clinal conditions prevail? Is it valid to exclude from systematic availability these genetic differences which do not happen to show complete dominance or which happen to be governed by a number of gene-sets? Are not all changes in genetic make-up of equal difficulty to instigate, regardless of how they express themselves? It seems to the writer that all differences in genotype should be available for taxonomic employment, regardless of their nature. The sole criterion of acceptability of any character should be that it be of a genotypic nature and not a phenotypic difference in response to environment. What the systematist is concerned with are the fundamental inheritable differences that exist between populations so that he can determine the true relationships of the latter to the end that a better under-

standing of the species in question can be accomplished.

Summary and Conclusions

The five morphological traits of the *americana* group of subspecies in the marten, recently analyzed geographically by Hagmeier (1958), are restudied. Each of the traits is reduced from five to three subdivisions and new maps are prepared. The present distribution of each trait is then studied and explained in the light of Wisconsin and post-Wisconsin events.

1. Stratification of morphologically different populations apparently took place during Wisconsin times and one population must have been isolated in the Rocky Mountains remote from the eastern zone of occupation.

2. A comparison shows that in this formerly glaciated area presently adjacent populations are not necessarily the most closely allied; in many instances very widely separated ones are more clearly derivable from a recent common source.

3. Subspecific naming of two of the present subspecies appears justifiable and after combination of two presently subspecifically-designated populations distinctive names appear valid in two other cases. In a final case involving the virtual identity of the Newfoundland variety with that in Alaska, nominal distinction between the two might be regarded valid on the basis of distance of separation.

4. Clinally distributed traits are shown to be acceptable for systematic usage in distinguishing subspecies.

REFERENCES

Burt, W. H. 1957. Mammals of the Great Lakes region. University of Michigan Press, Ann Arbor.

Cahalane, V. H. 1947. Mammals of North America. Macmillan, New York.

Dalquest, W. W. 1948. Mammals of Washington. Univ. Kansas, Publ. Mus. Natur. Hist., 2:1–444.

Davis, W. B. 1939. The recent mammals of Idaho. Caxton Printers, Caldwell, Idaho.

de Vos, A. 1952. The ecology and management of fisher and marten in Ontario. Ontario Department of Land and Forests, Ottawa.

Dillon, L. S. 1956. Wisconsin climates and life zones in North America. Science, 123: 167–176.

Hagmeier, E. M. 1958. Inapplicability of the subspecies concept to North American marten. Syst. Zool., 7:1–7.

Hall, E. R. 1926. A new marten from the Pleistocene cave deposits of California. Jour. Mammal., 7:127–130.

1931. Description of a new mustelid from the later Tertiary of Oregon. Jour. Mammal., 12:156–158.

Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. 2 vols. Ronald Press, New York.

Hopkins, D. M. 1959. Cenozoic history of the Bering land bridge. Science, 129:1519–1528.

Huxley, J. S. 1939. Clines; an auxiliary method in taxonomy. Bijdr. tot Dierkunde, 27:491–520.

Mayr, E., E. G. Linsley, and R. L. Usinger. 1953. Methods and principles of systematic zoology. McGraw-Hill Book Co., New York.

Rand, A. L. 1948. Glaciation, an isolating factor in speciation. Evolution, 2:314–321.

Rust, H. J. 1946. Mammals of northern Idaho. Jour. Mammal., 27:308–327.

Sibley, C. G. 1954. Subspecies and clines. The contribution of avian taxonomy. Syst. Zool., 3:105–110.

Swarth, H. S. 1936. Origins of the fauna of the Sitkan district, Alaska. Proc. California Acad. Sci., Ser. 4, Vol. 23:59–78.

Wright, P. L. 1953. Intergradation between *Martes americana* and *Martes caurina* in Western Montana. Jour. Mammal., 34:74–80.

L. S. DILLON is Associate Professor of Biology at Agricultural and Mechanical College of Texas, College Station, Texas.

The Classification of Endoparasitic Gastropods[1]

ELISHA S. TIKASINGH and IVAN PRATT

PARASITIC MOLLUSKS form a wide and diversified group. They are mainly parasites of echinoderms, but they also attack fishes (Unionidae), and even members of their own group (*Odostomia* on bivalves). The great majority of parasitic Mollusca are gastropods. Some look like typical gastropods with only a few organs lacking, while others are worm-like with nearly all their organ systems missing (Entoconchidae and Enteroxenidae). The one organ they all lack which is present in typical gastropods is the radula. It is for this reason that Thiele (1929) placed them all in his Stirps Aglossa under the Prosobranchia. This arrangement, however, is unsatisfactory, for the recent studies of Thorson (1946) and Fretter and Graham (1949) have shown that some of these gastropods are actually opisthobranchs.

The systematic position of the endoparasitic gastropods is still more difficult to determine, because nearly all organ systems are absent in the adult stage. However, several species have been described and need to be arranged systematically. J. Müller (1852) described *Entoconcha mirabilis,* the first parasitic gastropod, in *Leptosynapta* (*Lapidoplax*) *digitata,* but did not recognize it as such. However, Baur (1864) gave a fuller description in his discussion of *Helicosyrinx parasita.* Many species of these highly modified gastropods have since been described. Voigt (1888) described a new genus *Entocolax,* somewhat similar to *Entoconcha. Entocolax ludwigii* Voigt is found with one end attached to the body wall of *Myriotrochus rinkii* (Apoda: Myriotrochidae) in the Bering Sea. This end of the parasite maintains contact with the outside through a small opening. The other end is attached to a blood vessel. *Entocolax schiemenzii* Voigt is similarly attached to *Chiridota pisanii* (Apoda: Chiridotidae), off Chile (Voigt, 1901). Three additional species of *Entocolax* have been described: *Entocolax trochodotae* Heding (1934), from *Trochodota purpurea* (Apoda: Chiridotidae), *Entocolax schwanwitschi* Heding and Mandahl-Barth (1938) in *Myriotrochus eurycyclus* (Apoda: Myriotrochidae) from the Kara Sea, and *Entocolax rimsky-korsakovi* Ivanov (1945b) in the body cavity of *Myriotrochus mitsukuri* (Apoda: Myriotrochidae) from the Sea of Japan.

Enteroxenos östergreni Bonnevie (1902) is a more highly modified species of gastropod. It is usually attached to the intestine, but at times may lie freely in the body cavity of *Stichopus tremulus* (Aspidochirota: Stichopodidae), found in Norwegian waters. This species has also been investigated cytologically by Bonnevie (1904, 1906). Mandahl-Barth (1941) found several highly modified specimens which he described as *Thyonicola mortenseni* in the abyssal holothurian, *Thyone serrata* (Dendrochirota: Cucumariidae), off the Cape of Good Hope.

[1] Taken in part from a thesis submitted to the Department of Zoology, Oregon State College, in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Supported in part by a National Science Foundation Training Grant, administered by the Department of Zoology, University of Washington. Published with the approval of the Monographs Publications Committee, Oregon State University, as Research Paper No. 398, School of Science, Department of Zoology.

Parenteroxenos dogieli has been the object of several papers written by Ivanov (1945a,b, 1947a,b, 1948, 1949a,b). However Baer (1951) considered this species to be a synonym of *Thyonicola mortenseni* Mandahl-Barth.

Gasterosiphon deimatis[2] Koehler and Vaney (1903), a somewhat less modified snail, is found attached to the inside body wall of the abyssal holothurian *Deima blakei* (Elasipoda: Deimatidae). *Paedophoropus dicoelobius* Ivanov (1933, 1937), a shell-less snail, but nevertheless retaining its visceral hump and most of its organs, was found to occupy the polian vesicle of *Eupyrgus pacificus* (Molpadonia: Molpadidae). Certain species of melanellids are also known to be parasites of holothurians. Habe (1952) found several species of *Balcis* in the coelom or on the surface of a number of Japanese holothurians. *Megadenus holothuricola* Rosen (1910) was reported from the respiratory tree of *Holothuria* (*Ludwigothuria*) *mexicana* (Aspidochirota: Holothuriidae) from the Bahamas and Zanzibar. Because we lack first-hand information on this group, we are omitting them from the present discussion.

The only reports of endoparasitic gastropods occurring in North American waters are those of Dean (1896) and Harrington and Griffin (1897). In both papers the authors discuss the rediscovery of *Entoconcha* by the Columbia University Zoological Expedition of 1896 to Puget Sound, Washington. Recently, however, Tikasingh (1961) described *Comenteroxenos parastichopoli* from the holothurian *Parastichopus californicus* (Aspidochirota: Stichopodidae) and *Thyonicola americana* from *Eupentacta quinquesemita* and *E. pseudoquinquesemita* (Dendrochirota: Cucumariidae), both from Puget Sound, Washington.

Fischer (1883) proposed a section Parasita, under the order Opisthobranchiata, suborder Nudibranchiata, to include the genus *Entoconcha,* in the family Entoconchidae. Bonnevie (1902) described *Enteroxenos,* a second genus which she placed likewise in Entoconchidae. Schwanwitsch (1917) subdivided the family Entoconchidae into two subfamilies. "Entoconchini" and "Enteroxenini," placing *Enteroxenos* in the latter subfamily.

On the basis of hermaphroditism, the presence or absence of an intestine, differences in spermatozoa, differences in the embryonic shells and in the ontogenetic development, Mandahl-Barth erected a new family for *Enteroxenos,* the Enteroxenidae. Ivanov (1949b), however, claimed that the erection of two subfamilies or two families for this group of parasitic mollusks is "superfluous" and that the "Entoconchidae present a united natural group, the members of which are bound to one another by a series of transitions" (authors' translation). Further, he stated that the genera *Entocolax, Entoconcha, Thyonicola,* and *Enteroxenos* possess very close phylogenetic relationships.

In view of this controversy it is well to review here the structures on which the families are based. According to Mandahl-Barth (1938), the genera *Entoconcha* and *Entocolax* have "dwarf males," which possess a bladder-like testis together with a rudimentary vas deferens and a rudimentary intestine. However, he has not found the source of the "dwarf males" and they could have arisen from the gonad of the parasitic form, as is common among protandric hermaphrodites. The possibility that they came from outside the pseudopallium through the siphonal opening must be considered. However, until the developing "dwarf males" are observed outside the pseudopallium of the parasitic form as organisms arising directly from zygotes, it is more logical to assume that they arose hermaphroditically from the gonad of the parasitic stage

[2] This gastropod was originally named *Entosiphon,* but Koehler and Vaney (1905) later changed the generic name because it was preoccupied.

within the pseudopallium. Therefore, we consider these forms protandrous hermaphrodites.

Mandahl-Barth (1938), further stated that the spermatozoa of *Enteroxenos* are different from those of *Entoconcha* and *Entocolax;* the latter two he said are quite similar to each other. Ivanov criticized this with the statement that results of earlier workers were obtained by crude techniques. Ivanov's criticism is justified particularly since much more refined techniques in cytology have been introduced since Müller's time. A comparative study of the spermatozoa using modern techniques, however, may not reveal much more detail. It should be pointed out that some gastropods possess two types of spermatozoa, and it is quite possible that Mandahl-Barth was not comparing the same kinds. One of us found two types of spermatozoa in *Comenteroxenos*: one, with the typical conical head and long tail, the eupyrene type, and another more rodlike which was interpreted as an oligopyrene type sperm.

Mandahl-Barth continued his comparisons with the embryonic shells. His argument here does withstand Ivanov's criticism. *Entoconcha* and *Entocolax* possess shells with a slight tendency to spiral, but shells of *Enteroxenos* and *Thyonicola* are almost cucumber-like in appearance with no tendency to spiral. Ivanov (1949) maintained that this is to be expected since *Enteroxenos* and *Thyonicola* represent the last stages in the degeneration of these mollusks. However, we doubt that this is of importance in determining evolutionary relationships.

Another argument for the separation of the mollusks into two families is that *Entoconcha* and *Entocolax* both possess a short intestine, although no anus is present. No trace of intestine is seen in *Enteroxenos, Thyonicola,* and *Comenteroxenos.* Since an intestine represents an organ of primary importance, we believe its condition a good criterion for the separation of these two groups, especially when there are other supporting characteristics. We believe, therefore, that two families as set up by Mandahl-Barth should be maintained. These have the following characteristics:

Family Entoconchidae

1. Presence of "dwarf males" in pseudopallium (protandrous hermaphrodites?)
2. Larval shells with tendency to spiral.
3. Intestine present.

Family Enteroxenidae

1. Permanently hermaphroditic.
2. No tendency of shells to spiral.
3. Intestine absent.

Fischer (1883) proposed placing the Entoconchidae in the order Opisthobranchiata, suborder Nudibranchiata, section Parasita. Thiele (1929), in his classification of the mollusks, placed these forms with the prosobranchs, but Mandahl-Barth (1941) returned them to the Opisthobranchia. We conclude also that they are opisthobranchs. Further, since the characters of these two families do not fit those of any of the seven orders proposed by Odhner (1939) and since the definition of Stirps Aglossa of Thiele (1929) is for a group of tall-spired parasitic snails into which the Entoconchidae do not fit either as larvae or adults, we are reviving the order Parasita to include the families Entoconchidae and Enteroxenidae, following the intention of Fischer (1883). We are removing Parasita from Nudibranchiata and making it an order of Opisthobranchia. Ordinal characteristics: vermiform animals with most organ-systems missing; shell present in juvenile stages only and with only a slight tendency to spiral; hermaphroditic; pseudopallium well-developed; ctenidium and radula missing; parasites of echinoderms.

The contents of the two families follows:

Family Entoconchidae Fischer, 1883
(= *Cochlosyringia* Voigt, 1888)
Entoconcha mirabilis Müller, 1852
(= *Helicosyrinx parasita* Baur, 1864)
Entocolax ludwigii Voigt, 1888
Entocolax schiemenzii Voigt, 1901
Entocolax trochodotae Heding, 1934
Entocolax schwanwitschi Heding and Mandahl-Barth, 1938
Entocolax rimsky-korsakovi Ivanov, 1945

Family Enteroxenidae Heding and Mandahl-Barth, 1938
Enteroxenos östergreni Bonnevie, 1902
Comenteroxenos parastichopoli Tikasingh, 1961
Thyonicola mortenseni Mandahl-Barth, 1941
Thyonicola americana Tikasingh 1961

We, therefore, reject Ivanov's idea of one family for the entire group. We do agree with Ivanov that there is progressive modification of the parasites commencing with *Entoconcha* and ending with *Enteroxenos*. However, this argument can be carried out further if one starts with the family Melanellidae, where only a few organs are missing, such as the radula, and then on to the family Enteroxenidae, the members of which are highly modified. Yet, Ivanov probably would not agree that this whole realm of parasitic gastropods should be placed in one family. By the extension of the ideas of Ivanov, then, an orthogenetic type of evolution may have occurred starting with *Entoconcha* and ending with *Enteroxenos*, with *Thyonicola* as an intermediate form. The two families mentioned above should not necessarily be regarded as a situation in which one is derived from the other, for it is quite possible that they may have evolved separately and convergent evolution has brought them together as similar forms.

REFERENCES

Baer, J. G. 1951. Ecology of animal parasites. Univ. of Illinois Press, Urbana, 224 pp.

Baur, A. 1864. Beiträge zur Naturgeschichte der *Synapta digitata*. III. Die Eingeweideschnecke (*Helicosyrinx parasita*) in der Leibeshöhle der *Synapta digitata*. Nova Acta Acad.Leopold.Carol., 31:1–119.

Bonnevie, K. 1902. *Enteroxenos östergreni*, ein neuer, in Holothurien schmarotzender Gastropode. Zool. Jahrb., Abt. Anat., 15: 731–792.
1904. Zur Kenntnis der Spermiogenese bei den Gastropoden (*Enteroxenos östergreni*). Biol. Zentralbl., 24:267–274, 306–310.
1906. Untersuchunger über Keimzellen I. Beobachtungen an den Keimzellen von *Enteroxenos östergreni*. Jena. Zeitschr. Naturwiss., 41:229–428.

Dean, B. 1896. The Columbia University Zoological Expedition of 1896. Trans. New York Acad. Sci., 16:33–42.

Fischer, H. 1883. Manuel de conchyliologie et de paléontologie conchyliologique, deuxiéme partie: 517.
1889. Decouverte d'un nouveau type de Mollusques Gastropodes entoparasites (*Entocolax*). Jour. Conchyliol., 37:101–105.

Fretter, V., and A. Graham. 1949. The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. Jour. Marine Biol. Assoc. U. K., 28:493–532.

Habe, T. Parasitic gastropods found in echinoderms from Japan. Publ. Seto Marine Biol. Lab., 2:73–86.

Harrington, N. R., and B. B. Griffin. 1897. Notes on the distribution and the habits of some Puget Sound invertebrates. Trans. New York Acad. Sci., 16:152–165.

Heding, S. G. 1934. *Entocolax trochodotae*, n. sp., a new parasitic gastropod. Vidensk. Meddel. Dansk Naturhist. Forening, 98: 207–214.

Heding, S. G., and G. Mandahl-Barth. 1938. Investigations on the anatomy and systematic position of the parasitic snail *Entocolax* Voigt. Medd. om Grønland, 108: 1–40.

Ivanov, A. V. 1933. Ein neues endoparasitisches Mollusk, *Paedophoropus dicoelobius* n. gen., n. sp. Zool. Anz., 104:161–165.
1937. Die Organisation und Lebensweise der parasitischen Molluske *Paedophoropus dicoelobius* A. Ivanov. Acta Zoologica, 18: 111–208.
1945a. A new endoparasitic mollusk *Parenteroxenos dogieli* nov. gen., nov. sp. Dokladi Acad. Sci. URSS, 48:450–452.
1945b. *Entocolax rimsky-korsakovi* nov. sp., a new mollusk parasitic of *Myriotrochus mitsukuri*. Dokladi Acad. Sci. URSS, 49:534–536.
1947a. On the ways of penetration into the host body as observed in parasitic gastropods. Trudy Leningrad. Obsh. Estestvois., Otdel. Zool., 69:88–92 (Russian text, English summary).

1947b. The structure and the development of the endoparasitic mollusk *Parenteroxenos dogieli*. I. The organization of the adult animal. Izvest. Akad. Nauk SSSR, s. Biol., 1:3–29 (Russian text: English summary).
1948. On the metamorphosis of the parasitic mollusk, *Parenteroxenos dogieli*. Dokladi Acad. Nauk SSSR, 61:765–768 (in Russian).
1949a. The structure and development of the endoparasitic mollusk *Parenteroxenos dogieli*. II. Organisation of the larva and postlarval metamorphosis. Izvest. Akad. Nauk SSSR, s. Biol., 2:109–134 (in Russian).
1949b. The structure and the development of *Parenteroxenos dogieli*. III. On the relations among the genera of Entoconchidae. Izvest. Akad. Nauk SSSR, s. Biol., 2:135–139 (in Russian).

KOEHLER, R., and C. VANEY. 1903. *Entosiphon deimatis*. Nouveau mollusque parasite d'une holothurie abyssale. Revue Suisse Zool., 11: 23–41.
1905. Deep sea Holothuroidea collected by the Investigator. Echinoderma of the Indian Museum III.

MANDAHL-BARTH, G. 1941. *Thyonicola mortenseni* n. gen., n. sp., eine neue parasitische Schnecke. Vidensk. Meddel. Dansk Naturhist. Foren., 104:341–351.

MÜLLER, J. 1852. Uber die Erzeugung von Schnecken in Holothurien. Müller's Archiv, No. 1 (Transl. Ann. Mag. Natur. Hist., ser. 2, vol. 9:103–112).

ODHNER, N. H. 1939. Opisthobranchiate Mollusca from the western and northern coasts of Norway. Kong. Norske Vidensk. Selsk. Skrifter, Nr. 1, pp. 1–92.

ROSÉN, N. 1910. Zur Kenntnis der parasitischen Schnecken. Acta Univ. Lund, N.F., Afd. 2, 6:1–67.

SCHWANWITSCH, B. N. 1917. Observations sur la femelle et le mâle rudimentaire d'*Entocolax ludwigii*. Jour. Russe Zool. 2:1–147.

THIELE, J. 1929. Handbuch der systematischen Weichtierkunde. I. Gustav Fischer, Jena, 376 pp.

THORSON, G. 1946. Reproduction and larval development of Danish marine bottom Invertebrates. Medd. Komm. Danmarks Fiskeri-og Havundersøgelser, ser. Plankton 4, No. 1, 523 pp.

TIKASINGH, E. S. 1961. A new genus and two new species of endoparasitic gastropods from Puget Sound, Washington. Jour. Parasitol. 47:268–272.

VOIGT, W. 1888. *Entocolax ludwigii*, ein neuer seltsamer Parasit aus einer Holothurie. Zeitschr. Wiss. Zool., 47:658–688.
1901. *Entocolax schiemenzii* n. sp. Zool. Anz., 24:285–292.

ELISHA TIKASINGH is a Rockefeller Fellow at the Trinidad Regional Virus Laboratory, Port-of-Spain, Trinidad. **IVAN PRATT** is Professor of Zoology at Oregon State University, Corvallis, Oregon.

Distance as a Measure of Taxonomic Similarity[1]

ROBERT R. SOKAL[2]

Introduction

THE LAST FEW YEARS have seen the development of a number of methods for quantifying the classificatory process in systematics (Michener and Sokal, 1957; Sokal and Michener, 1958; Sokal, 1958; Sneath, 1957a; Sneath, 1957b; Cain and Harrison, 1958; Rogers and Tanimoto, 1960). These sudden developments, largely independently arrived at, appear to stem from a growing dissatisfaction with the arbitrariness and subjectivity of the customary taxonomic procedure and would also appear to be connected with the increasing availability of rapid methods of data processing and computation. In spite of certain differences among them, these methods show substantial philosophical and procedural agreements. They call first of all for the computation of a measure of resemblance or similarity between taxa. Resemblances are computed between every pair of taxa in a given study and these resemblances are arranged in the form of a so-called Q-type matrix, which is a matrix of similarities among taxa. These matrices are subsequently analyzed by various types of cluster or factor analysis and in this manner the structure and degree of relationships among taxa are revealed. These methods have been called "quantitative systematics" in the past. Recently Sokal and Sneath have renamed them collectively as "numerical taxonomy" (Sokal, 1960).

The computation of taxonomic similarity depends on several assumptions. The most important of these are (1) that the evaluation of similarities among taxa is based on the observed values of characters and not on phylogenetic speculations and interpretations. Hence taxonomic affinities or similarities are *phenetic* rather than phyletic. (2) The similarities are evaluated on the basis of many characters and all characters are considered to be of equal taxonomic value; hence no one character is weighted more or less than any other character.

Three types of coefficients have been suggested to date as suitable measures of similarity between pairs of taxa. These measures can be conveniently classified as coefficients of association, correlation, and distance. Coefficients of association are generally restricted to characters subdivided into two states only. These are the so-called "present-absent" characters employed in various types of ecological association coefficients and first applied to taxonomic work by Sneath (1957b). Coefficients of association vary considerably in the details of their formulation, but are based on an arrangement of the data in the form of a 2 x 2 table. The coefficient of correlation which has been employed in numerical taxonomy (Sokal and Michener, 1958; Morishima and Oka, 1960) has been of the ordinary Pearson

[1] Contribution No. 1096 from the Department of Entomology, The University of Kansas, Lawrence, Kansas.

[2] This work was done while the author was a Senior Postdoctoral Fellow of the National Science Foundation (U.S.A.) at the Galton Laboratory, University College, London. He would like to express his appreciation to the Foundation for its support and to Professor L. S. Penrose, F.R.S., for his hospitality and encouragement. Prof. C. D. Michener and Mr. F. James Rohlf of The University of Kansas have read this manuscript and suggested improvements.

product-moment type, permitting the characters to be subdivided into more than two states.

The third type of coefficient determines the similarities between two taxa as a function of their distance in an n-dimensional space whose coordinates are the characters. The present paper will elaborate on this particular approach.

The use of distance as a measure of taxonomic similarity is not new. The earliest application that I have been able to locate is by Heincke (1898) working on herrings. A similar method was employed by Anderson and Abbe (1934) in comparing specific and generic differences in the birches. Zarapkin's (1934) work is related indirectly to the concept of distance. Distance was extensively employed to summarize the resemblances between samples of anthropological material. This work resulted in the formulation by Karl Pearson (1926) of the coefficient of racial likeness from which has sprung the concept of the generalized distance suggested by Mahalanobis (1936) and further elaborated by Rao (1952). In a later section of this paper the relation of these statistics to the simple distance proposed here as a measure of taxonomic similarity will be discussed. In 1958 Cain and Harrison suggested a so-called "mean character difference" which was not interpreted as a distance by them but which is mathematically related to the concept of distance as will be shown below.

The Computation of Distance

Let us assume that we are studying two species, 1 and 2, which are described on the basis of two characters X and Y. Characters X and Y are measured; if continuous, and numerically coded in other cases. The two species may have any value for X and Y within the range of variation of these characters. Then we can plot our data as in Figure 1, where each of the two species assumes a fixed position in the two-dimensional space defined by the two axes X and Y. A measure of the similarity between species 1 and 2 based on the two characters would be the distance in the two-dimensional space (i.e. on the plane) between the two species. Thus the greater the distance the less the two species would resemble each other. This distance $\delta_{1,2}$ can easily be computed by means of a well known formula of analytical geometry,

$$\delta_{1,2}=\sqrt{(X_1-X_2)^2+(Y_1-Y_2)^2},$$

where X_1, Y_1 are the coordinates of species 1. This formula is often conveniently stated in its squared form in order to avoid the square root on the right side. Therefore,

$$\overset{2}{\delta}_{1,2}=(X_1-X_2)^2+(Y_1-Y_2)^2$$

which is the same as the formula given in Figure 1. When we wish to describe three characters for the two species we have to use a three-dimensional figure (a cube) in order to represent the exact position of the two species with respect to the three characters. This cube is shown in a two-dimensional projection in Figure 2. The computation of the distance between the two species, which are now suspended at fixed points in the three-dimensional space, is by an extension of the distance

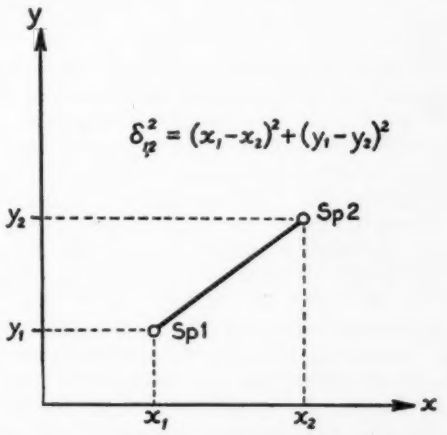

FIG. 1. Two-dimensional diagram showing the distance between two hypothetical species with reference to two characters, X and Y.

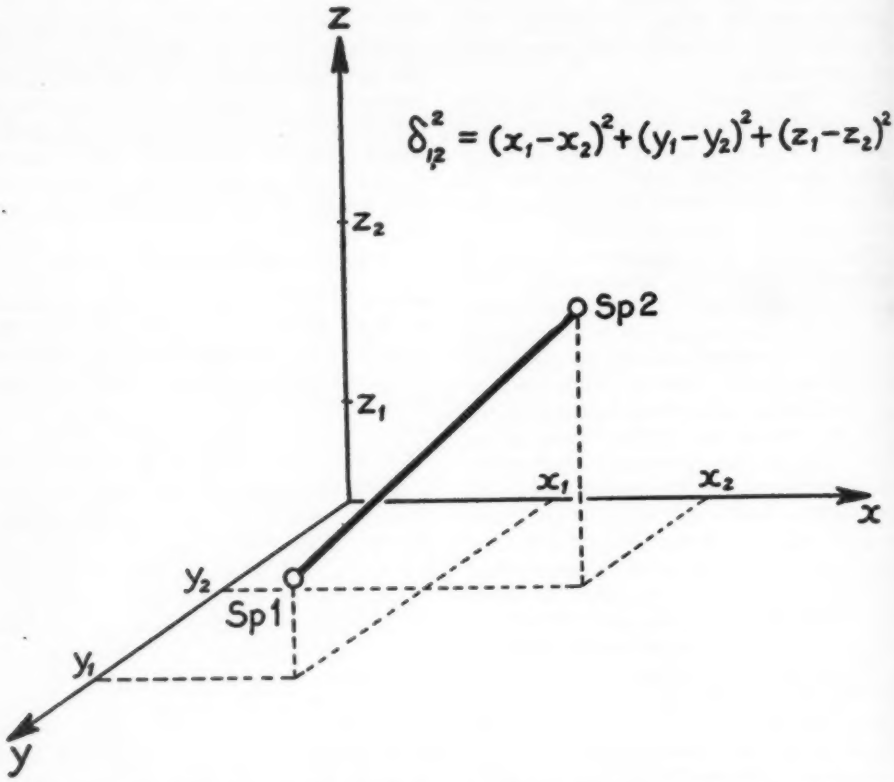

FIG. 2. Two-dimensional projection of the distance between two species with reference to three characters, X, Y, and Z.

formula previously discussed and the square of the distance is as shown in Figure 2. As soon as we describe species on the basis of more than three characters we are no longer able to depict their positions and relationships in a conventional diagram and we are forced to rely on algebraic manipulation of the data. However, the distance formula of analytical geometry is equally valid in an n-dimensional space (i.e., a hyperspace). The squared distance between two species in such a hyperspace of n characters can be computed very simply by summing the squares of the distances along each of the n axes (characters).

We may generalize the formula for the distance squared of two species and n characters as follows:

$$\delta^2_{1,2} = \sum_{i=1}^{n} (X_{i1} - X_{i2})^2$$

where X_{i1} is the state code of species 1 for character i.

Such a distance formula can be applied to characters divided into two or more states. The number of states per character can vary from character to character. If the original data are set up in matrix form, as seems conventional in numerical taxonomy, with the columns of the matrices representing species (or other taxa) and the rows representing characters, then the distance squared is

simply the sum of the squares of the differences between any pair of columns. For computational purposes, either on a desk calculator or by means of electronic computation, it would probably be best to calculate the squared differences in the following form:

$$\delta^2_{1,2} = \sum_{i=1}^{n} X_{i1}^2 + \sum_{i=1}^{n} X_{i2}^2 - 2\sum_{i=1}^{n} X_{i1}X_{i2}.$$

Such computations are extremely simple. For a reasonable number of taxa with simply coded character states they would not present a prohibitive amount of work, even if only a conventional desk calculator were available for processing the data. See Appendix for a computational example.

Modifications of the Procedure

The actual distance between taxa (or the square of the distance between them) is necessarily a function of the number of characters for which the taxa are compared. Other factors being equal, the greater the number of characters involved in the comparison, the greater the distance between taxa. While within a given study (i.e., between a number of taxa which are being compared simultaneously) the number of characters will remain constant and hence the distances will give a relative evaluation of taxonomic similarity, it would be preferable to use some generally acceptable standard by means of which these distance coefficients would be compared. It would therefore seen appropriate to divide the sum of the squared differences by n, the number of characters on which it is based, obtaining a mean squared difference,

$$\overline{\delta^2}_{1,2} = \frac{1}{n}\sum_{i=1}^{n}(X_{i1} - X_{i2})^2,$$

which seems appropriate as a general measure of the taxonomic distance. It is immediately apparent that this quantity is merely the variance of the differences between the character state codes of the two taxa being compared. If preferred, the square root of the above expression, representing the standard deviation of the differences may be employed.

In this connection it is desirable to discuss the relation of $\overline{\delta^2}_{1,2}$ to the mean character difference (M.C.D.) proposed as a measure of taxonomic similarity by Cain and Harrison (1958). The M.C.D. can be summarized by the following formula:

$$\text{M.C.D.(between taxa 1 and 2)} = \frac{1}{n}\sum_{i=1}^{n} |X_{i1} - X_{i2}|.$$

Thus it is the average of the absolute differences between the character state codes of two taxa. It is therefore in the same relation to the distance coefficient proposed above as the average deviation, frequently used in the early days of statistics, is to the standard deviation. It shares some of the disadvantages of the earlier statistic. Thus it will always be less than the true distance and will not permit the partitioning which is possible in mean squares.

Readers familiar with Pearson's coefficient of racial likeness (C.R.L.) will have noticed the similarity of the distance coefficient proposed here to the coefficient employed by Pearson (1926). The latter is conveniently formulated (in its squared form) as follows:

$$\text{C.R.L. (between taxa 1 and 2)} = \frac{1}{n}\sum_{i=1}^{n}\left\{\frac{(m_{i1} - m_{i2})^2}{\frac{s^2_{i1}}{n_1} + \frac{s^2_{i2}}{n_2}}\right\} - \frac{1}{n}$$

where n is the number of characters for which the two taxa are compared, m_{i1} is the mean for character i in taxon 1, s^2_{i1} is the variance for character i in taxon 1 and n_1 is the number of individuals in taxon 1 from which the mean and variance have been computed.

As already mentioned above Pearson's formulations, which were employed to

measure the resemblances among anthropological material (mostly skulls), led to the development of more refined techniques, the generalized distance procedures of Mahalanobis (1936) and Rao (1952). Pearson's coefficient and the generalized distance procedures are not appropriate for the usual type of work in numerical taxonomy, since in the latter field we use a single code value to represent the state of a given character in a given taxon. We do not therefore consider variation for a given character within a taxon. On the other hand, the material with which Pearson and the Indian statisticians were dealing had characters which were largely continuous, varying with the population, and in their attempts to compute distance coefficients for such material they had to take into account the mean and variance of each of the characters considered. Since the material with which we are working consists to an appreciable proportion of discontinuous characters and since there is in many cases no variation of the particular state code within the taxon the problem of intrataxon variation in state codes does not usually arise in our data and we may assume their values to be fixed. Furthermore as a matter of simple practicality we cannot consider the methods of generalized distance in the study of numerical taxonomy, since these methods require inversions or similarly involved operations on matrices of the order of the number of characters considered. As we are often considering as many as a hundred or more characters the inversions of such matrices would be entirely impractical. No claim is made here that the characters which we are considering in numerical taxonomy are always invariable within taxa. On the contrary; in low ranking taxonomic units, such as subspecies, races, or varieties, as well as high ranking taxa, many character states are not constant for the entire taxon. How such data should be treated will be discussed in a forthcoming publication.

A further modification is desirable in the distance coefficient as proposed here. Since the coding of the various characters is arbitrary and since the range of state codes is therefore likely to vary from as little as one to as much as eight, nine, or even more, or since measurements can be in different units, the possible maximum distance between taxa on the various axes is likely to vary, and consequently unequal consideration of the various characters is likely to be introduced in the computation of a measure of taxonomic similarity. It would therefore be desirable to standardize the characters in some prearranged fashion in order to have the range of variation identical for all characters used in the study. Cain and Harrison (1958) dealt with this problem when they used the maximum expression of a character as 100% and arbitrarily graded all other expressions of the character as some portion of this total percentage. A difficulty attending this practice is that with the introduction of new taxa exhibiting more extreme expression of certain characters, the entire taxonomic material would have to be recoded and the study recomputed, since the new state codes would have to be a recalculated fraction of the new maximum expression of the character.

It would seem preferable to standardize the variation of characters in the customary manner by standardizing each row of the initial data matrix, i.e., all state codes for one character in a given study are transformed to possess a mean of zero and a variance of 1. This is easily accomplished by subtracting from each state code the mean state code for that character and dividing the difference by the standard deviation of the state codes for this character. This operation can be performed automatically when the data are fed into a digital computer or it can quite simply be performed on a desk calculator before the actual distances are computed. When the computations are carried out on a desk calculator it would be desirable to code the data in such a manner as to keep

them all positive in order to avoid having to use negative values (see Table 6, Appendix). It is, of course, true that by this procedure the inclusion of a new taxon exhibiting characters more extreme in their expression than those in the previous study will also provide some computational difficulty. However, if, as is likely, we can assume that the variance of the character is not too different, we can express it as a deviation from the previous mean of the character state codes using the previous standard deviation, unless we have too many new additions to the particular study.

The formula for distance squared of standardized state codes is:

$$\overline{\delta^2}_{1,2} = \frac{1}{n} \sum_{i=1}^{n} (\xi_{i1} - \xi_{i2})^2,$$

where ξ_{i1} is the standardized state code of taxon 1 for character i. When we compare the above formula with the formula for Pearson's coefficient of racial likeness for standardized data (see Penrose, 1954),

$$\text{C.R.L. (between taxa 1 and 2)} = \frac{1}{n} \sum_{i=1}^{n} (\xi_{i1} - \xi_{i2})^2 - \frac{1}{n},$$

we note that the two are almost identical.

If all the characters chosen are functions of general size it may be that size will exert an undue influence on the determination of phenetic similarity. In such instances standardization of the columns in the original data matrix should follow the standardization of the rows and is likely to remove bias of this sort.

Evaluation

We do not as yet have comparative studies indicating the relative merits of the various types of coefficients in numerical taxonomy. It is obvious that the relation of the coefficient of distance to coefficients of correlation and association is a complementary one. The larger the distance, the smaller the degrees of association or correlation between taxa. In discussions with various taxonomists I have found that the concept of distance is one that appears more appealing to them than the concepts of correlation and association. It is also somewhat simpler to visualize; through the two- and three-dimensional model the idea of distance between taxa can be grasped easily. Distances are related to the type of result obtained in comparative serological studies. See for example Boyden (1958). From the point of view of computation the distance coefficient is not as easy to compute as an association coefficient, but is rather easier than a correlation coefficient, at least on a desk calculator. A digital computer will probably handle distances and correlations equally rapidly. At the University of Kansas we are at present preparing a program which will handle both correlations and distances simultaneously. The use of this program will permit us to evaluate the relative outcomes of the two methods. Persons interested in using such a program, which will be written for the IBM 650 digital computer with floating decimal arithmetic and index registers, are invited to contact the author.

In structuring the matrix of the coefficients of similarities based on distance we can use the customary methods of cluster analysis. Ordinary methods of factor analysis, which have proven useful in describing classifications and arranging the taxa in a hierarchic system, will not work on distance data as such. However, various methods of multivariate analysis should be able to partition the matrix of distances into its significant components.

Objections may be raised to using an orthogonal coordinate system to plot the distances between taxa, when we know that rows representing characters are correlated. This is a fundamental problem of all Q-type analysis in psychology as well as biology. At this time it is proposed to continue the use of characters as independent information. However, a

study of evaluating the effects of correlation of rows on structure in a Q-type study is planned.

Summary

A coefficient of distance between taxa is proposed as an alternative measure of resemblance or similarity in numerical taxonomy. This distance can be computed as the mean sum of squares of the differences between standardized character state codes of the taxa concerned.

REFERENCES

ANDERSON, E., and E. C. ABBE. 1934. A quantitative comparison of specific and generic differences in the Betulaceae. Jour. Arnold Arboretum, 15:43–49.

BOYDEN, A. 1958. Comparative serology; aims, methods and results. *In* Serological and Biochemical Comparison of Proteins, XIV Annual Protein Conference, W. Cole (ed.) Rutgers University Press, New Brunswick, pp. 3–24.

CAIN, A. J., and G. A. HARRISON. 1958. An analysis of the taxomist's judgment of affinity. Proc. Zool. Soc. London, 131:85–98.

HEINCKE, F. 1898. Naturgeschichte des Herings. I. Abhandl. Dtsch. Seefischerei-Vereins, 2.

MAHALANOBIS, P. C. 1936. On the generalized distance in statistics. Proc. Nation. Inst. Sci. India, 12:49–55.

MICHENER, C. D., and R. R. SOKAL. 1957. A quantitative approach to a problem in classification. Evolution, 11:130–162.

MORISHIMA, H., and H. OKA. 1960. The pattern of interspecific variation in the genus *Oryza;* its quantitative representation by statistical models. Evolution, 14:153–165.

PEARSON, K. 1926. On the coefficient of racial likeness. Biometrika, 18:105–117.

PENROSE, L. S. 1954. Distance, size and shape. Ann. Eugenics, 18:337–343.

RAO, C. R. 1952. Advanced statistical methods in biometric research. John Wiley and Sons, New York.

ROGERS, D. J., and T. T. TANIMOTO. 1960. A computer program for classifying plants. Science, 132:1115–1118.

SNEATH, P. H. A. 1957a. Some thoughts on bacterial classification. Jour. Gen. Microbiol., 17:184–200.

1957b. The application of computers to taxonomy. Jour. Gen. Microbiol., 17:201–226.

SOKAL, R. R. 1958. Quantification of systematic relationships and of phylogenetic trends. Proc. Tenth Internation. Congr. Entomology, 1:409–415.

1960. Die Grundlagen der numerischen Taxonomie. Proc. Eleventh Internation. Congr. Entomology (in press).

SOKAL, R. R., and C. D. MICHENER. 1958. A statistical method for evaluating systematic relationships. Univ. Kansas Sci. Bull., 38: 1409–1438.

ZARAPKIN, S. R. 1934. Zur Phänoanalyse von geographischen Rassen und Arten. Arch. Naturgesch., new ser., 3:161-186.

ROBERT R. SOKAL is Associate Professor in the Department of Entomology at the University of Kansas, Lawrence.

Appendix

Some readers may find a computational example helpful. I have chosen the small, fictitious example employed by Cain and Harrison (1958) to illustrate the computations for the mean character differences. Table 1 gives the value of the character

TABLE 1—TAXA

		A	B	C	D	E	$\sum_{j=1}^{t} X_{ij}$	$\bar{X}$
Characters	1	100	90	95	5	10	300	60
	2	100	85	80	5	5	275	55
	3	75	100	95	20	15	305	61
	4	5	5	0	80	100	190	38
	5	90	100	—	20	25	235	58.75
	6	100	50	25	—	—	175	58.33
	7	90	95	100	0	0	285	57
$\sum_{i=1}^{n} X_{ij}$		560	525	395	130	155		
$\sum_{i=1}^{n} X_{ij}^{2}$		51850	46875	35075	7250	10975		

Character state codes for seven (n) characters of five (t) hypothetical species (taxa) from data by Cain and Harrison (1958). Maximum expression of a character is represented by 100, its absence by 0. Missing information is symbolized by a hyphen.

states for seven characters and for five species (taken from Table 1 of Cain and Harrison).

Table 2 gives differences and differences squared between taxa *A* and *B*. The sum of the squared differences, 3575, can also be obtained from the formula

$$\delta^2_{A,B} = \sum_{i=1}^{n} X^2_{1A} + \sum_{i=1}^{n} X^2_{1B} - 2\sum_{i=1}^{n} X_{1A}X_{1B}$$

$\sum_{i=1}^{n} X^2_{1A}$ is obtained by squaring and summing column *A* of Table 1, $\sum_{i=1}^{n} X^2_{1B}$ by similar treatment of column *B* (Table 1). $\sum_{i=1}^{n} X_{1A}X_{1B}$ is the sum of the products of columns *A* and *B*. (Table 2). Hence $\delta^2_{A,B}$ will be 51,850 + 46,875 − (2)47,575 = 3575. The mean squared differences $\overline{\delta^2_{A,B}}$, is obtained by dividing $\delta^2_{A,B}$ by n, the number of characters. Therefore $\overline{\delta^2_{A,B}} = 3575/7 = 510.7$. The theoretical maximum of $\overline{\delta^2}$ for any pair of taxa in this instance is clearly 10,000. Thus taxa *A* and *B* are quite closely related. Where there are missing values for certain character states, as in taxa *C*, *D*, and *E*, the deviations are taken only where applicable and are divided by the number of differences employed. Thus $\overline{\delta^2_{C,D}} = 35,750/5 = 7,150$, as can be seen from Table 2.

If we wish to standardize the state codes for each character (i.e., each row of the original data matrix) we proceed as follows. We first subtract the mean of each row (shown in Table 1) from each character state code in that row as shown in Table 3. These new rows will consequently add up to zero (as shown near the right hand margin of Table 3). Then we calculate the sum of squares of each coded character. Since the mean is zero, the sum of squares of character i is simply $\sum_{j=1}^{t} X^2_{ij}$, and the variance is that quantity divided by the number of taxa, t, over which this row has been summed. The standard deviation and its reciprocal value are calculated next. Table 4 shows each coded character state value (from Table 3) divided by the standard deviation (or multiplied by its reciprocal). These are the standardized state codes ξ. From them we can calculate $\overline{\delta^2_{j,k}}$ as before. The matrix of distance coefficients is given in Table 5. The expected value for the average distance squared between two randomly picked taxa is $(1.12)^2 = 1.2544$. Thus we find that some coefficients e.g., $\overline{\delta^2_{A,B}}$, are much less than expected, i.e., the taxa are very closely related, while others, e.g., $\overline{\delta^2_{B,E}}$, are much farther apart than expected, i.e., the taxa are not closely related.

The necessarily negative values of some standardized character state codes may lead to computational errors when the work is carried out on desk calculators. Coding the data by adding a constant 5 to all values in Table 4 would remove this difficulty (see Table 6). The reader can easily convince himself that the values of $\overline{\delta^2_{j,k}}$ calculated from Table 6 are identical with those calculated from Table 4.

TABLE 2

	$(X_{1A}-X_{1B})$	$(X_{1A}-X_{1B})^2$	$X_{1A}X_{1B}$	$(X_{1C}-X_{1D})$	$(X_{1C}-X_{1D})^2$
Characters 1	10	100	9000	90	8100
2	15	225	8500	75	5625
3	−25	625	7500	75	5625
4	0	0	25	−80	6400
5	−10	100	9000	—	—
6	50	2500	5000	—	—
7	−5	25	8550	100	10000
$\sum$		3575	47575		35750

Some intermediate computational steps for obtaining $\overline{\delta^2_{A,B}}$ and $\overline{\delta^2_{C,D}}$ as explained in the text.

TABLE 3—TAXA

	A	B	C	D	E	$\sum_{j=1}^{t} X_{ij}$	$\sum_{j=1}^{t} X_{ij}^2$	s_x^2	s_x	$1/s_x$
Characters 1	40	30	35	—55	—50	0	9250	1850	43.01	.02325
2	45	30	25	—50	—50	0	8550	1710	41.35	.02418
3	14	39	34	—41	—46	0	6670	1334	36.52	.02738
4	—33	—33	—38	42	62	0	9230	1846	42.97	.02327
5	31.25	41.25	—	—38.75	—33.75	0.00	5318.7500	1329.69	36.46	.02743
6	41.67	—8.33	—33.33	—	—	0.01	2916.6667	972.22	31.18	.03207
7	33	38	43	—57	—57	0	10880	2176	46.65	.02144

Character state codes from Table 1 with the row mean subtracted from each code. Computational steps for standardizing rows.

TABLE 4—TAXA

		A	B	C	D	E	$\sum_{j=1}^{t} X_{ij}$
Characters	1	.9300	.6975	.8138	—1.2788	—1.1625	0
	2	1.0883	.7255	.6046	—1.2092	—1.2092	0
	3	.3834	1.0679	.9310	—1.1227	—1.2596	0
	4	—.7680	—.7680	—.8843	.9774	1.4429	0
	5	.8571	1.1314	—	—1.0628	—.9257	0
	6	1.3364	—.2672	—1.0690	—	—	0.0002
	7	.7074	.8146	.9218	—1.2219	—1.2219	0

Character state codes of Table 1 standardized by rows.

TABLE 5

	A	B	C	D	E
A	—	.4732	1.0655	2.7979	4.0242
B	.4732	—	.1191	4.0760	4.3145
C	1.0655	.1191	—	3.9896	4.4011
D	2.7979	4.0760	3.9896	—	.0446
E	4.0242	4.3145	4.4011	.0446	—

Matrix of squared distance coefficients between taxa of Table 4.

TABLE 6—TAXA

		A	B	C	D	E
Characters	1	5.9300	5.6975	5.8138	3.7212	3.8375
	2	6.0883	5.7255	5.6046	3.7908	3.7908
	3	5.3834	6.0679	5.9310	3.8773	3.7404
	4	4.2320	4.2320	4.1157	5.9774	6.4429
	5	5.8571	6.1314	—	3.9372	4.0743
	6	6.3364	4.7328	3.9310	—	—
	7	5.7074	5.8146	5.9218	3.7781	3.7781

Standardized character state code of Table 4 coded by addition of 5 to avoid negative values.

An International Taxonomic Register: Preliminary Proposals

WILLIAM L. BROWN, JR.

Introduction

IT IS MY BELIEF that our present method of recording the basic data of animal (and plant) taxonomy is inefficient and uneconomical—in a word, it is obsolescent. Nowhere is this more obvious than in systematic entomology, for it is particularly in the insects, along with the spiders and mites, that the bulk of publication has swollen to such unmanageable proportions. Let us look at the dimensions of the problem so far as insects alone are concerned.

Each year, some 10,000 new species and genera of insects are described and named (estimate by C. W. Sabrosky, in litt.), and this number is increasing instead of decreasing. Each year, an additional large number of older names is put into synonymy, and many other standing species and genera are redescribed, figured for the first time, or are reported in significant new range extensions, etc. Each year, the publication of this material fills countless expensive pages in hundreds, perhaps thousands, of scientific periodicals, memoirs, bulletins, books, and pamphlets, each with a total circulation ranging from a few dozen copies to many thousands. It seems safe to say that the large majority of such publications have circulations of less than 1,000, and 500 is probably more like an average figure. The subscriberships are often worldwide, but some are surprisingly local, too.

No one library, even among the most alert and affluent institutions of Europe or North America, can hope to hold a current and complete set of all the world's taxonomic literature, because many of the issuing agencies are both obscure and ephemeral, and they often have neither the resources nor the inclination to guarantee really wide distribution. Yet the new species published in such marginal sources may be perfectly valid under the International Rules, provided only that a few vague and rather modest requirements for distribution are met. It is my guess that any zoologist hoping to find under one roof publications containing half or more of the new species of animals described during the year, say, 1959, would have to choose among less than 100 libraries in the entire world, most of them situated in a few restricted areas of Europe and North America. If this zoologist lives very far from one of the 100 libraries, chances are that he is out of luck for the literature he needs.

For most practical purposes, the task of recording in some manner the vast outpouring of basic zoological systematics has been left to one agency: the Zoological Record. Considering its meager financial resources, the small company of compilers of the Record have done an heroic job over the years, and they deserve the earnest thanks of zoologists everywhere. Still, without the least intention to criticise or minimize the efforts of its compilers and editors, I must affirm what every taxonomist knows, namely, that the Zoological Record is far from an ideal register of zoological systematic materials. It is usually behind the current literature by two, three, or more years, and many references, species and (especially) new synonymies, are missed altogether. Considering the obscurity, unavailability, and slowness of issue of many organs con-

taining taxonomic proposals, the lag and the omissions of the Record are clearly inevitable.

Even when a species or genus does enter the Record listing, it is still accompanied only by a bare minimum of reference data plus, usually, the country of provenience of the types. Then follows for many users the frustrating task of securing the data from the actual article in which the description or synonymy occurs. I have found new species of ants listed in the Zoological Record from little-known works published in Moravia, Japan, and Uruguay, of which I was unable to find a single copy in any library in North America, even though all of these publications were issued during the years since World War II. In these cases, reprints, excerpts, or photocopies were obtained only after months of inquiry, correspondence, and the efforts of several librarians, and then at no inconsiderable expense. This was all done from the base of one of the world's most complete zoological libraries, in the institution in which I was fortunate enough to be working. Most taxonomists are less well off; it is amazing how many institutions—colleges, museums, experiment stations, and so forth—carry on zoological-systematic research without even the Zoological Record. A colleague of mine recently went to join the faculty of a college on the Pacific Coast, where, since he was to be the only entomologist, the faculty library committee had decided to take their first entomological journal so as to honor the new man's specialty. My friend, who is an insect taxonomist and morphologist, was proudly shown the new entomological holding of the library—The Journal of Insect Physiology!

An active specialist on any large taxon of animals must keep some kind of list, file, or catalog of the genera and species within the taxon. Printed catalogs of reasonably recent date are available for only a fraction of insect taxa, and even these are frequently limited to particular sections of the earth. Catalogs vary markedly in quality and completeness, and their usefulness, of course, declines with each year following their compilation; supplements to catalogs are awkward at best. The average catalog takes many tedious man-years to complete, and its publication can be counted on to be both costly and slow. A card catalog file, if it is complete for both the newer and the older literature, can be exceedingly useful. But if the taxon is large, the drudgery of maintaining even a current file may consume half or more of a specialist's precious research time. As a result, personal taxonomic files are seldom really complete and up-to-date, and many workers prefer to bear the very serious risk of not maintaining one at all.

I could go on and list many other shortcomings of the present system of recording and storing taxonomic information, but only at the risk of boring those readers who live with these problems in their daily research. What I should like to do here is to ask, and then try to give one answer, to the question: what should we do about it?

Outline of a Proposal for an International Taxonomic Register

We need an international register that will receive, record, and publish basic taxonomic data. Publication should be in unit form, by separate taxa. This means that each description of a new species or genus, each proposal of a new synonymy, each new combination, etc., would be published on a separate card. With modern microcard or similar techniques, the descriptive or explanatory text and figures for one new taxon can easily be reduced just enough to fit on one card. Brief descriptions, synonymies, generic transfers, and the like might be printed with little or no reduction by offset directly on the cards.

The register would be absolutely complete for current publication. The heart of the plan is the provision that would ensure the completeness, which is that

the register would be designated as the sole source of publication for priority purposes of new taxa (as well as new synonymies and so on). After a given starting date, priority for any authorship and name of a taxon newly described would date from the day of registry, which could be made to correspond to the date of issue of the card. Cards could be mailed out periodically, perhaps by the month or quarter, to subscribers who would be free to order at cost all cards issued, cards for particular orders or families, or even single cards by serial number. The registration, publication, and distribution of the cards would be performed by a central registry having clerical and mailing functions, but no editorial jurisdiction. Material for publication in the register would be edited by (a) a panel or single judges, consisting of experienced taxonomists for each major taxon, elected by the active workers in that taxon, or (b) the editors of any of the scientific journals of the class which now publishes acceptable descriptions, etc., under the International Rules. The editorial provision is designed to ensure freedom of publication at least as broad as that prevailing at the present time.

For the subscribers, the file of cards would constitute a permanent, expandable catalog which, through economical photographic techniques now available, could eventually be extended backward to cover the older literature and provide a complete file for any group of animals. Of course, definite possibilities exist for the modification of such a file system by building into the cards recovery and crossfiling properties, but that is a refinement I have not pursued for now.

Administrative and Financial Problems of an International Registry

An international registry could naturally be started only after receiving support from an overwhelming majority of working taxonomists. This support will not be marshalled tomorrow, we can be sure, but I believe that an arrangement more or less like that just proposed will inevitably come sometime, and we can best prepare by giving it serious thought right now. The registry would have a set of ground rules or a constitution, established by worldwide agreement—possibly reached through an international poll. After this hurdle is cleared, the registry proper would be set up to operate in as nearly automatic a fashion as possible to handle the purely mechanical jobs of manufacture and distribution of the cards. In other words, the registry itself would perform functions normally those of the printers in conventional scientific publication, and would be responsible for nothing else beyond storage of a master set of cards and duplicate copies. The editors would be free and independent agents, operating in essentially the way they do now in conventional journals. The editor's name could appear somewhere on the cards he has passed for publication. No more of the International Rules should apply to registrant authors than now applies to authors of conventionally published articles and books. The director of the registry could be responsible either to a board of the editors or their representatives or to an international board of working taxonomists. The cards could appear in any of the languages now considered acceptable in world taxonomy. Proof copies would be submitted to both editor and author for final reading and correction before issue.

The location of a registry would have to be considered, but with the rapidity and efficiency of the world's mails today, the registry could operate in any one of several stable, literate, industrial nations. Editors, of course, could work anywhere.

The method of financing the registry would depend on the total cost, for which there cannot yet be any really solid final figures. The present cost of manufacture of one microcard (with up to 40 typewritten sheets on it, or twice that many printed octavo sheets) is about seven

cents, assuming an issue of 500 cards or more. Mailing costs would be additional to this, as would certain editorial expenses, even assuming that the editors receive no pay for their labors. At present, we might expect that cards might cost in the neighborhood of ten cents apiece, though this is a very tentative estimate. It is felt that the system, once it got started under public or private subsidy, might become nearly or completely self-supporting through subscription alone. It is possible that future costs of cards may go down, particularly if the volume of production were to reach the proportions needed to cover the Animal Kingdom or a class as large as the insects.

As a rough example of possible costs, let us take the published data for the ants (family Formicidae) during the year 1958; the figures of course are approximate only.

New taxa described	100
New synonymies proposed	200
Generic transfers, etc.	100
Total	400

This would be about 400 cards which, at .10 per card, would cost $40. In this case, the large number of new synonymies (200 for one year) reflects revisionary trends after several decades of rather ill-considered and excessive description; within a few years, the new-synonymy rate will have settled to a fraction of its present figure, and the total entries for this family will drop to perhaps 200 per year. At any rate, brief descriptions, many new synonymies, most generic transfers, and the like will contain so little material to be reproduced that the cards for these might be printed by cheaper photo-offset at a cost well below ten cents apiece. Thus, the total cost to the subscriber of a file containing all basic taxonomic data on ants for a given year might be expected to run from about $10 to $40, on the assumption that the registry is run without subsidy. This cost is within range of what many taxonomists now pay for subscriptions to entomological journals—journals now made up of from ¼ to ⅓ of material that could be expected to appear on cards if the register were operating. This would represent a possible means of balancing off the cost of register subscription, and it should not be forgotten that even blank 3 x 5 file cards cost about two-tenths of a cent apiece these days. Other substantial savings to the subscriber could be made on catalogs, abstracting journals, and reprints that he would otherwise need to buy and store. Many smaller colleges, museums, and other institutions supporting some systematic research that could not afford to subscribe to a complete set of zoological cards each year could nevertheless easily pay for those sections directly needed for staff research in progress; and thus avoid most of the library problems that always arise on a small budget. And in figuring costs in time and money, we should not forget the expenditures that go with the building and maintenance of a personal file or checklist.

Summary of Advantages of an International Register Card File System

Advantages to the Author

Convenience of Publication. It would allow immediate unit publication as soon as descriptions, new synonymies, new names, generic transfers, etc., are completed. These need not be held until the monograph or revision of which they are a part is published. This means that monographs and revisions, normally consisting largely of formal descriptive material, will be reduced to manageable size, and the keys, phylogeny, zoogeography, ecology, behavior, and other general aspects of the group under consideration will form the main part of the work and will be relatively more accessible and attractive to general readers. Furthermore, the compilations and correlation

needed for the completion of the general parts of a monograph are more easily made from handy file cards than from sequentially-paged books or monographs or manuscripts. In these days of high publishing costs, a monograph pared to the more general (and more widely useful) conclusions, keys, etc., would be much more attractive to prospective sources of publication than would the bulky old-style monograph with every species and every locality record in its place among the pages. Finally, it should be recalled that under the system proposed here, a wider choice of editors would be available to the author than is now the case.

Distribution. Authors could count on an average wider distribution than they now have for descriptive works, and a more effective distribution in terms of reaching specialist users more rapidly and directly.

Bibliography. An international card file would greatly simplify, or in some cases eliminate, basic taxonomic bibliography citations.

Publication costs. Cost of printing, reproduction of figures, etc., would be defrayed automatically in the process of registration, and would not, as it often now does, fall upon the author.

Reprints. Since presumably most or all of those interested in the basic data on the cards would themselves be taxonomists and subscribers to the register, the expense and trouble of reprints of this material would be eliminated.

Advantages to Taxonomic Users

Completeness. The international register file would be absolutely complete for current description, and could conveniently be expanded to include older taxa so as to approach or reach completeness for all species of any taxon.

Convenience. It would eliminate time-consuming literature searches and the need for making personal files. A card file is easily stored and maintained as compared to standard journals, or even reprints. Cards can be arranged in any desired fashion for storage or for active use, i.e., in taxonomic or phyletic order, by food plants, by geographical distribution, and so on, and they can be compared with one another or with specimens with a minimum of difficulty. Cards can be annotated on their backs, cross-filed, and readily mailed. A card file system could eventually be modified for mechanical retrieval.

Economy. An international card file would eliminate the expense of some subscription to conventional journals, and would also do away with the need for most abstracts, catalogs, checklists, and reprints of purely basic taxonomic interest, as well as storage and maintenance of these items.

Simplification of Reference Citations. Example: *"X-us albus* T. M. Smith 1960 R." "R" would stand for "International Taxonomic Register." It might be prudent to cite the serial number also in some cases.

Advantages to Science in General

Improvement of Periodical Publications. The register would eliminate the cost to journals, etc., of most descriptions and figures, and would allow them to publish more information on taxonomic conclusions of general interest, and more material on ecology, behavior, physiology, zoogeography, etc. In this way, general reader interest could be increased. It is expected that many of the smaller or *ad hoc* publications would no longer be necessary, and some smaller entomological journals, for instance, might merge. It is surprising how many journals exist primarily as vehicles for the description of new taxa.

Abstracts and Catalogs. Under the register system, the need for abstracting publications such as the taxonomic section of the Zoological Record and of the Biological Abstracts, insofar as these organs list references to basic descriptions

and so forth, would disappear. Conventional taxonomic catalogs would be eliminated, thus saving tremendous amounts of time, energy, and money. The catalog services of libraries everywhere would benefit by the simplification of taxonomic references.

Revisions and Monographs. As already mentioned above, comprehensive monographic works, or essentially non-taxonomic papers that include some descriptions of novelties, would be shortened and simplified through relegation of many purely taxonomic data to register publication. Thus simplified, such works would be easier to use by everyone, and would cost much less to publish. The publication of summary works would thus be greatly stimulated and encouraged.

Summary

It is proposed that taxonomists, and particularly arthropod taxonomists, begin to consider the possibility of establishing an international taxonomic register through which all "official" descriptions of new species, proposals of new names, generic transfers, and other basic formal data would be published and distributed on unit cards suitable for forming a catalog file.

WILLIAM L. BROWN, JR., is Assistant Professor of Entomology at Cornell University, Ithaca, New York.

Higher Categories and Phylogeny.[1]

R. S. BIGELOW

A RECENT controversy over the taxonomic boundary between mammals and reptiles (Olson, 1959; Simpson, 1959, 1960; Van Valen, 1960; Reed, 1960) has called attention to difficulties that arise when fossil evidence becomes extensive. These difficulties are due to an *abundance* of evidence and will not, therefore, disappear as our knowledge grows. They will increase. We cannot brush these difficulties lightly aside, and we should search for a system of classification that will reduce their extent.

Our current classifications have been built on a "horizontal" foundation. Most of our higher category concepts spring directly from an awareness of contemporary forms. For example, the very name "Mammalia" refers to a characteristic that can be observed directly in living forms only, and mammals are also defined by their hair, warm blood, diaphragm, etc. Fossils were added gradually, as they were discovered, to pre-existing arrangements of living forms. Our higher category concepts grew backward, from the present into the past.

Most contemporary organisms can be segregated into a number of large assemblages with relative ease. Intermediates between birds, mammals, and reptiles are very rare among living forms; zoologists are virtually unanimous in referring the echidna and the duckbill to the Mammalia. Children can learn to distinguish between the Lepidoptera, Diptera, Coleoptera, and Hymenoptera. Entomology students quickly learn to recognize families within these ordinal groups despite the fact that a larger number of apparently intermediate forms makes this more difficult. It is only with the lower categories that taxonomic gaps begin to disappear.

All this is well known to biologists. The taxonomic gaps between the higher categories exist because the extinct, ancestral, intermediate forms no longer exist. These gaps are not only useful in classification, they are also meaningful in terms of evolution; they should be recognized and used, both for taxonomic convenience and as food for evolutionary thought. Any system of classification that tends to obscure these gaps, or even to obliterate them, should be re-examined closely.

The reference of fossils and living forms to the same higher category groupings tends toward the obliteration of even the widest taxonomic gaps. If all the animals that have ever lived were known to us, extinct ancestors would form a continuum with existing forms and *all* our taxonomic boundaries would have to be drawn arbitrarily. Even though most ancestors have left no trace of their former existence, fossil evidence is already sufficiently complete in some groups to create difficulties, and there is every reason to expect that future studies and discoveries will reveal similar problems in other groups. For example, when all the fossil insects that are now awaiting study in the museums of the world have been studied thoroughly, entomologists might well find themselves face to face with as many problems as now confront mammalian paleontologists.

The problem of the Mammalia–Reptilia boundary is a good example of the difficulties that follow the reference of fossils and existing forms to the same higher category groups. The taxonomic boundary between these two great classes was at

[1] Contribution from the Faculty of Agriculture, Macdonald College, McGill University, Quebec, Journal Series No. 467.

first clear and distinct, but it has become progressively less distinct as fossils have been discovered, until today there is a difference of opinion between authorities that spans about 70 million years and involves a great multitude of mammal-like reptiles (or reptile-like mammals, according to one's point of view).

Olson (1959) and Simpson (1959) draw a boundary between mammals and reptiles in the upper Triassic, leaving therapsids in the Reptilia, Van Valen (1960) draws this boundary in the lower Triassic, 50 million years or so earlier, including the therapsids in the Mammalia. Reed (1960) extends the class Mammalia back beyond the Mesozoic altogether, to the lower Permian, including not only the therapsids but even their sphenacodont pelycosaur ancestors in the Mammalia! Reed is of course aware of the fact that pelycosaurs were *not* mammals, but he is apparently convinced that full attainment of a monophyletic "ideal" is more desirable than taxonomic logic. Full attainment of the "ideal" requires the inclusion of the one species that all mammals share as a common ancestor in a single vertical class with all its descendants, however many perfectly natural groups are thereby broken up, and however unlike its descendants this one original species may have been.

The significance of Reed's proposal tends to escape us. Most of us are not as familiar with Permian pelycosaurs as we are with our contemporary mammals; we tend to overlook the fact that Reed is placing pelycosaur species that belong in the same genus into different classes. We can perhaps appreciate the full enormity of this if we can imagine leaving lions in the Mammalia while transferring tigers to the Reptilia.

Reed (1960) is not unaware of this inherent weakness in vertical, monophyletic classification. He says:

> "It is quite true that, considered in time-depth, horizontal classification is always more convenient. Vertical classification typically results in removing one adaptive line from a number of evolving lines of an adaptive radiation and including that one line in another taxon for the reason that the one line differed from its brother lines by having a potentiality that led to a major new taxon. Vertical classification in practice is thus generally most inconvenient to the working paleontologist."

One is inclined to ask why Reed, despite his awareness of the superiority of horizontal classification in both logic and convenience, recommends such a strict adherence to the illogical and inconvenient system of vertical classification. He does so, apparently, because he agrees with Huxley (1958, 1959), who suggests that we should select either clades or grades (vertical or horizontal groupings) for our formal system of classification. Huxley focussed attention on the fact that horizontal and vertical classification are two distinct and different *kinds* of classification which should not be confounded. Reed agrees, and says: "Logically, there is no middle ground, but our taxonomic principles now wander in that illogical middle ground, and will probably remain there for some time." He selects the vertical principle as the fundamental basis for establishing a taxonomic category, and recommends adherence to this principle regardless of logical consequences. Although I agree with Reed that a choice should be made, I disagree with his choice. Reed himself has made it clear that the illogical area is not confined to the middle ground; vertical classification *typically* separates "brother lines" on the basis of their evolutionary potentialities alone. Reed did not, however, make it clear that strict adherence to the monophyletic "ideal" would also bring together categories that should be separated on the basis of every other evolutionary criterion. If we are to include the entire mammalian family tree, including the single ancestral species shared by all, in the class Mammalia we should, to be consistent, do the same with the class Reptilia. This would return not only the Permian pelycosaurs, but even horses, cats, dogs, men, and all birds to the class Reptilia. If we are really consistent, the entire lot

must be placed in the class Amphibia, along with frogs and salamanders, or in a piscine class. We must either add ever higher categories at one end of the scale or else reduce the Mammalia (including pelycosaurs) to generic rank. Consistent monophyleticism would require the inclusion of birds and crocodiles in a single group from which lizards and turtles are excluded, or the inclusion of men with coelocanths in a group that excludes salmon and perch. It would, in fact, result in taxonomic chaos.

Horizontal classification, on the other hand, is not only absolutely necessary in the case of living forms, but it is recognized by Reed himself as more convenient, even for *paleontologists*. Simpson and Olson favor horizontal principles when they refuse to include therapsids in the Mammalia. Even Van Valen favored horizontal principles when he refused to include pelycosaurs in the Mammalia. Whenever a higher category boundary is shifted toward descendants and away from ancestors on the basis of overall similarity, horizontal principles are favored over vertical principles. Simpson (1960) rejected the proposals of Reed and Van Valen on the grounds that the monophyletic ideal should not be stretched to the point of absurdity. He pointed out that Reed's proposal is probably wrong by Reed's own (monophyletic) principles, and that insistence on strict monophyly might require the inclusion of amphibians, or perhaps even fishes, in the class Mammalia. Simpson's somewhat looser definition of monophyly (descent from a group of lower categorical rank) is clearly more logical than Reed's uncompromising interpretation of the term, and Simpson's compromise is a step toward a horizontal system.

However, the same argument that Simpson uses for rejecting Reed's proposal can be used for rejecting an arrangement that Simpson has accepted. Simpson (1953) made the following statement:

> "Matthew pointed out, but later students have mostly ignored the fact that eohippus was *not* a horse, that it is about as good an ancestor for *Rhinoceros* as for *Equus*. In effect, there was no family Equidae when eohippus lived. The family and all its distinctive characters developed gradually as time went on. Eohippus is referred to the Equidae because we happen to have more nearly complete lines back to it from later members of this family than from other families. There is no particular time at which the Equidae became a family rather than a genus or a species; the whole process is gradual and we assign the categorical rank after the result is before us."

If eohippus was not a horse it should not be called a horse, any more than a Permian pelycosaur should be called a mammal. If there was no family Equidae when eohippus lived the relegation of eohippus to the Equidae is as difficult to justify as the relegation of pelycosaurs to the Mammalia. If Simpson's Equidae is acceptable, then Reed's Mammalia is also acceptable, on the same grounds. It is not surprising that Matthew's advice was ignored because Simpson did, in fact, refer eohippus to the Equidae. Neither is it surprising that we have to be reminded of the fact that eohippus is about as good an ancestor for *Rhinoceros* as for *Equus*, because its relationship to *Rhinoceros* is obscured by its having been placed in the Equidae. It is very clear that not only "students" and Reed, but also Matthew and Simpson, have been led astray by vertical classification.

We cannot escape the conclusion that vertical classification fails to qualify as a logical and convenient formal system. The purpose of classification is the arrangement of data in such a way as to facilitate a maximum number of valid inferences concerning those data. The best classification of living organisms is one that will facilitate biological studies of *all* kinds. An arrangement that favors one kind of study at the expense of another is less desirable than one that facilitates all kinds of study equally. For example, an arrangement that facilitates studies of horse evolution but tends to obstruct studies of rhinoceros evolution is less desirable than one which facilitates studies of both horse

and rhinoceros evolution simultaneously and equally. This cannot be achieved without a surrender of vertical "ideals"; nothing will be gained by favoring rhinos instead of horses, and our only choice is to shift the family Equidae "upward," into a time when "the result is before us," and out of the Eocene, when Simpson says it did not exist. Any such shift is a step toward horizontal principles.

Horizontal classification presents one major difficulty: it can be applied to only one horizontal array of contemporaries at a time. Taxonomic gaps in basic, overall similarity will tend to correspond with the rank of the categories they separate at any one level of time, but whenever the categories are extended backward in time the gaps will begin to disappear. The logical extreme of horizontal classification is an infinite series of hierarchies corresponding with each single instant of time. Although this is more logical than a strictly monophyletic arrangement of all organisms that have ever lived, neither "ideal" is attainable and we are forced to compromise. Simpson's compromise is clearly a step in the right direction, but we should strive toward greater improvement.

For example, all Eocene animals might be placed in a separate Eocene hierarchy of higher and lower categories. This would not eliminate the irrationalities of vertical classification altogether, but it would greatly reduce them. The Equidae, for example, would not be present; there would be no need to place one eohippid in the Equidae and another in another family. Pelycosaurs would also be absent. The clade leading to horses would not be favored over that leading to rhinos; the arrangement as a whole would be less prejudiced in favor of the best known clades. A series of horizontal hierarchies would facilitate the highly important study of clades. The line leading from pelycosaurs to modern mammals could still be expressed, but as a *clade*, not as the class Mammalia.

A series of horizontal hierarchies would automatically show the temporal relationships between ancestors and descendants. Standard prefixes (e.g., P, Q, R, S, T, and U for the Paleocene to the Pleistocene respectively) would automatically align fossils according to their occurrence in time. This is an essential first step in the study of any clade, and it is not achieved by our present system. In cases of slow evolution, where certain descendants of a given group (say, a family) persist without change through several geological periods, one could still use the same family name and change only the prefixes.

Interactions between the contemporaries that coexist at any one time play a significant rôle in the evolution of their descendants, and every array of contemporaries is different from every other array of contemporaries. The woolly mammoth no longer affects the evolution of other animals and plants; pterodactyls and birds did not coexist in the Eocene; whales and ichthyosaurs did not coexist in the Mesozoic. The reciprocal effects of predator and prey, insects and flowering plants, etc., are produced only by the action of contemporaries on other contemporaries. A series of horizontal hierarchies would assist studies of the selective forces acting at any one time, and of the gradual changes in these forces that occurred with the passage of time. Our present system confounds ancestors and descendants and therefore obstructs studies of these selective forces.

Although it is impossible to completely remove the arbitrary component from classification, it could be reduced. The arbitrary boundaries between the various eras, periods, etc., must be dealt with in any case. Decisions as to whether a given fossil lived in the Jurassic or the Cretaceous cannot be evaded whatever system of classification is favored. If these same temporary boundaries were to be used also as arbitrary boundaries between successive horizontal hierarchies no *new* arbitrary element would be introduced, but

a myriad of arbitrary boundaries between genera, families, classes, etc., would be eliminated. Under the present system such boundaries must ultimately be drawn, on morphological evidence, between animals that belong in the same genus on morphological evidence. Under the present system, we must deal with *both* the time zone boundaries *and* the higher category boundaries. Recognition of the time-zone boundaries alone would therefore reduce the arbitrary element in classification. Boundaries set between the time zones would be frankly and obviously arbitrary; they would not imply extensive morphological gaps that do not exist, but merely temporal differences that *do* exist. Fossils from intermediate formations could be referred, with notations, to both formations with justification. A fossil found at the Jurassic-Cretaceous boundary, for example, was almost certainly descended from very similar ancestors that lived in the Jurassic, and left very similar descendants that lived in the Cretaceous.

Although it is often difficult to determine whether a given formation was laid down in the Cretaceous or the Jurassic it is rarely difficult to distinguish between the Cretaceous and the Permian, or between the Permian and the Eocene. However difficult such determinations might be, they must be made, and errors are just as serious under the present system of classification as they would be under any other system. Paleontologists refer fossils to the various periods with an air of confidence. A considerable array of fossils is known to have lived in the Jurassic, and a very different array is known to have lived in the Eocene. The task of arranging Jurassic, or Eocene, fossils into a single Jurassic (or Eocene) hierarchy should be less difficult than fitting these fossils into a single vast hierarchy that includes all organisms of all times. The classification of fossils in a series of hierarchical groupings *in accordance with the stratified series of rocks in which they were found* could hardly fail to correspond with evolution more accurately than the system in current use, and it would certainly be less arbitrary and less subject to errors of human judgment and prejudice.

The virtues and weaknesses of horizontal and vertical principles, and the way in which these two principles contradict one another, can be appreciated, in part at least, through a study of Figure 1. Each vertical column of this diagram may be considered as a single phyletic line, each "fork" in the "tree" as an appearance of reproductive isolation. The diagram is deliberately simplified to correspond with a monophyletic viewpoint, i.e., the effects of parallel evolution, and of unequal rates of evolution, are excluded. The various groupings at each time level are meant to correspond with both overall similarity and recency of common ancestry, simultaneously.

If we can imagine four uncompromising monophyleticists, one of which died shortly after Time 1, another shortly after Time 2, etc., it will be difficult to imagine

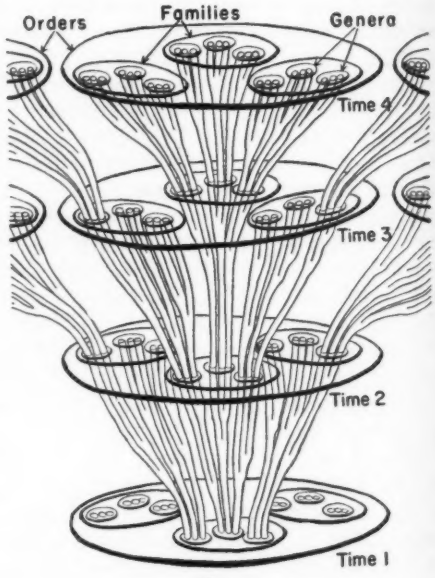

FIG. 1

agreement between these four men. The three species nearest the center of the diagram at Time 1 would be placed in the same genus by the Time 1 man, in three different genera by the Time 2 man, in three different families by the Time 3 man, and in three different orders by the Time 4 man.

It will not be difficult, on the other hand, to imagine agreement between four proponents of a series of horizontal hierarchies, each of which died shortly after each time level. In this case the perfectly natural groups at each time level would not be disrupted by any one of the four men, and the four hierarchies, considered together, would show that each group was descended from another group of lower categorical rank at the preceding level of time. Considered separately, each horizontal grouping meets the requirements of monophyletic classification, and a "horizontal monophyly" is achieved throughout the diagram. Vertical monophyly, applied to the entire diagram, will meet the requirements of monophyletic classification at Time 4 only; at all other levels of time the groupings will not be monophyletic.

As Simpson (1960) suggests, vertical classification tends to negate itself through its own principles, even where it does not have to deal with parallel evolution and unequal evolutionary rates. Any diagram that shows these two widespread phenomena would be more realistic than Figure 1, and would show even more clearly the weakness of vertical classification and the necessity for a series of horizontal hierarchies.

Dr. Everett C. Olson has stated (in correspondence) that he is disposed toward utility as a basis of judgment in choosing between any systems of classification. Many others, including myself, would agree with him. From a utilitarian standpoint horizontal classification is regarded as more convenient, even by Reed, and a series of horizontal hierarchies would:

(1) recognize the wider, easier to find, more meaningful and more logical taxonomic gaps between higher categories at different time levels,

(2) represent the gradual element in evolution more accurately by excluding eohippus, for example, from a non-existent Equidae,

(3) reduce the present tendency to concentrate attention on one clade at the expense of others,

(4) automatically align fossils according to their occurrence in time,

(5) facilitate studies of interactions between contemporaries, and

(6) reduce the arbitrary component in classification by concentrating it in the frankly arbitrary time boundaries already in use.

Horizontal and vertical classification represent two distinct and different, often contradictory, systems. We should, as Huxley and Reed suggest, select one or the other for our formal system of classification, and in making our choice we should not overlook the superiority of horizontal classification in utility, convenience, and evolutionary logic.

REFERENCES

HUXLEY, J. S. 1958. Evolutionary processes and taxonomy with special reference to grades. Uppsala Univ. Arsskrift, No. 6:21–39.

1959. Clades and grades. *In* A. J. CAIN (ed.) Function and taxonomic importance. Publication No. 3. The Systematics Association, Brit. Mus. (Nat. Hist.), London, pp. 21–22.

OLSON, E. C. 1959. The evolution of mammalian characters. Evolution, 13:344–353.

REED, C. A. 1960. Polyphyletic or monophyletic ancestry of mammals, or; What is a class? Evolution, 14:314–322.

SIMPSON, G. G. 1953. The major features of evolution. Columbia Univ. Press, New York.

1959. Mesozoic mammals and the polyphyletic origin of mammals. Evolution, 13: 405–414.

1960. Diagnosis of the classes Reptilia and Mammalia. Evolution, 14:388–392.

VAN VALEN, L. 1960. Therapsids as mammals. Evolution, 14:304–313.

R. S. BIGELOW is Associate Professor in Macdonald College, McGill University, Quebec, Canada.

Current Tendencies to Increase the Number of Higher Taxonomic Units Among Insects[1]

D. KEITH McE. KEVAN

Introduction

IT IS GENERALLY assumed that there has been a *recent* tendency among entomologists to increase the number of orders, families, and other higher taxa among insects, but a *current* tendency is not necessarily, *per se*, a recent one. In fact, where a trend toward such an increase currently exists, it would seem that it is most usually part of a gradual process that has been continuing for a long time. In recent times, however, there appears to have been a tendency for entomologists in general to *recognize* an increasing number of the insect families that have been accepted by specialists, often for many years, but not widely recognized by non-specialists.

There are varying opinions (even among specialists) on the desirability of affording recognition to this or that group at this or that level in the hierarchy, and many entomologists are averse to changing from whatever particular system was in vogue when they were students—the more so if they are not taxonomists—so that we are far from being able to approach this problem objectively. It is not, however, my intention to discuss very fully the functions and limitations of classificatory systems; this has been the subject of a recent article by Blackwelder (1959), among others.

In the space available it is obviously impossible to discuss all the categories used in the higher taxonomy of insects and the following remarks will be confined almost entirely to a consideration of orders and families. Categories between these two are, after all, merely used for grouping families showing some degree of affinity, while the arrangement of genera into tribes and subfamilies is mainly a tool of the specialist. Only the order and the family are primary categories and a consideration of the other categories would tend to complicate the discussion unduly.

The Number of Hexapod Orders

Since it is outside the purpose of this paper to discuss which animals should be regarded as insects and which should not, the less ambiguous term 'Hexapoda' will be used except when no ambiguity exists.

How many orders of Hexapoda are there then? Perhaps any individual entomologist could do a rapid mental calculation and give a fairly definite answer (which he would almost certainly quickly revise on remembering an order he had forgotten!), but I hazard a guess that if this simple question were put to any group of entomologists there would be a surprising lack of agreement. A glance at Table 1 would readily explain this, for there never has been any agreement on this point. For the purposes of this paper the year 1925 might be taken as a starting point for the modern era since it saw the almost simultaneous publication of three

[1] Contribution to a symposium entitled "Some basic aspects of systematic categories, mainly those above the species level," organized by the Entomological Society of America, held at Atlantic City, November 30, 1960. Macdonald College Journal Series No. 471.

TABLE 1—NUMBER OF ORDERS OF LIVING HEXAPODA RECOGNIZED BY VARIOUS AUTHORS.

Linné (1766–1767)	9	Berlese (1920)	11[1]	Weber (1938)	33
Latreille (1831)	12	Maxwell-Lefroy (1923)	26	Martynov (1938)	32
Westwood (1839–1840)	14	Handlirsch (1925)	33	Comstock (1940)	26
Packard (1882)	8	Imms (1925)	23	Essig (1942)	33
Kirby (1885)	7	Comstock (1925)	26[1]	Jeannel *in* Grassé (1949)	32
Brauer (1885)	18	Tillyard (1926)	24	Grandi (1951)	30
Sharp (1895–1899a)	10	Handlirsch et al. (1926–1938)	33	Borror and Delong (1954)	26
Sharp (1899b)	21	Brues and Melander (1932)	34	Brues et al. (1954)	27
Shipley (1904)	22	Weber (1933)	33	Ross (1956)	28
Börner (1904)	22	Imms (1934)	23	Imms et al. (1957)	29
Comstock and Comstock (1906)	19	Lameere (1934–1938)	24[3]	Maximum[4]	39
Handlirsch (1908)	35[1]				

[1] Including orders not placed in the Insecta, s.str., by the author cited.
[3] It is difficult to determine the exact status accorded to some of this author's categories.
[4] The full number recognized by Handlirsch (1908) with the addition of Protura, Zoraptera, Grylloblattodea, and Zeugloptera; none of the authors cited recognizes the last of these.

of the most influential general texts on entomology, or their relevant parts (four, if Berlese's *Gli Insetti* is included). The number of orders recognized at that time, however, varied from as few as 23[2] to as many as 34.

Continental European workers have tended to favor a larger, and traditionally conservative British workers a smaller, number of orders. American authors, without contributing much, appear to have been torn between the two schools, the majority probably having been led by J. H. Comstock into recognizing 26 orders. Brues and Melander (1932) and Essig (1942), whose work is consulted by a great number of students, however, have "rebelled" against the accepted pattern and followed the continental Europeans; Borror and Delong (1954), whose text is also widely used, on the other hand, still recognize only 26 orders.

Is there then a current tendency to increase the number of orders? Handlirsch (1908), at the beginning of the century, actually recognized more orders of hexapods than any subsequent author (even without the Protura, Zoraptera, Zeugloptera, and Grylloblattodea), but his system was a little too revolutionary (particularly in respect of apterygote groups) and at first was not accepted. After modification (Handlirsch, 1925), however, it had a very wide influence so that the number of orders recognized by continental Europeans has remained fairly stable, at a little over 30, ever since. British authors, on the other hand, to some extent influenced by the paucity of their native fauna, have only recently tended to recognize more orders than formerly. They are now more or less in line with other Europeans, although still a little more conservative (Imms et al., 1957). Americans continue to "pay their money and take their choice." Essig's text, listing 33 orders, has been issued in a new printing (1954) simultaneously with the appearance of that of Borror and Delong (1954), giving 26, whilst Brues and Melander (1932), in its contemporary revised edition (Brues et al., 1954), and Ross (1956) recognize intermediate numbers of orders. There is thus undoubtedly a certain fluidity in the situation, but a tendency to increase the number of orders there is not. On a world basis rather the reverse is the case.

One of the main reasons for the fluctuation in the number of orders is a purely subjective reluctance, justifiable or not, on the part of many entomologists to accept the necessity for recognizing numer-

[2] Berlese recognized only 11 but the taxonomic section of his work is very small and was written much earlier.

ous small or relatively small orders, members of which may be infrequently encountered, unfamiliar, or "unimportant." That the groups concerned are distinctive entities is seldom disputed, but whether they should be given ordinal status or not arouses controversy, which—as Blackwelder (1959) has pointed out—serves little purpose. Should the Raphidioptera and Megaloptera be given ordinal rank? Should the Blattodea (Blattaria), Mantodea, Grylloblattodea, and Phasmatodea be separated from the saltatorial Orthoptera, and, if so, how many orders should they represent? Are the Diploglossata Dermaptera or not? Should we recognize the Zeugloptera as having ordinal status, as suggested by Chapman (1917) and Hinton (1946), or, conversely, should the Strepsiptera be reunited with the Coleoptera as advocated by authors such as Lameere (1938) and Crowson (1955); or should we recognize but a single order Phthiraptera in place of separate Siphunculata and Mallophaga?

Only one really large group, the Hemiptera,[3] is seriously affected by this sort of controversy. Many authors, both European and American, have long treated the Homoptera and Heteroptera as separate orders, and this is undoubtedly convenient since the major subdivisions may be given subordinal rank, thus "tidying up" a rather cumbersome classificatory system. The somewhat intermediate position of the Peloridiidae, however, makes this course of action difficult to justify.

To sum up, then, it would seem that the tendency to increase the number of hexapod orders was current in the late nineteenth and early twentieth centuries rather than at the present time (see Table 1), and that the situation is now fluid. Some groups not widely recognized formerly as having ordinal status (particularly among the orthopteroids) are now being more generally accepted, while others widely regarded as belonging to distinct orders are being reunited (e.g., Homoptera and Heteroptera = Hemiptera).

[3] The Orthoptera (sens. lat.) also constitute a large group, but the "break-away" orders are minorities, even if some are sizable ones.

The Number of Hexapod Families

It can be seen by reference to various works which give more or less complete lists of families for all orders (see Table 2 [4]), that during the present century there has been a continuous rise in the number of families, and the inference is that this increase is continuing. It is also apparent that there are two schools of thought: one favoring a more conservative attitude, and the other tending to recognize large numbers of families—more or less up to the maximum proposed by various specialists. Thus, while we see a gradual trend exemplified by Sharp (1895-1899a), Handlirsch (1925), Imms (1925), Comstock (1925), Imms (1934), Grandi (1951), and Imms et al. (1951), showing a rise from about 270 families at the beginning of the century to over 680 at the present, we can also see the extremist tendency reflected by Brues and Melander (1932) and Brues et al. (1954) who recognize over 900 families.

[4] Only a selection is given to indicate general trends; some important works are omitted.

TABLE 2—NUMBER OF FAMILIES OF LIVING HEXAPODA RECOGNIZED BY VARIOUS AUTHORS.

Westwood (1839–1840)	178 [1]
Kirby (1885)	300+
Sharp (1895–1899)	270
Berlese (1920)	165
Handlirsch (1925)	326
Imms (1925)	416+
Comstock (1925)	450
Tillyard (1926)	433
Handlirsch et al. (1926–1938)	537
Brues and Melander (1932)	903
Imms (1934)	470+
Lameere (1934–1938)	340+
Comstock (1940)	450+
Grassé (Ed.) (1949–1951)	821
Grandi (1951)	504
Brues et al. (1954)	942
Imms et al. (1957)	680+

[1] Excluding "Aptera."

It is interesting to note, however, that while the conservatives, represented by the various editions of Imms, have permitted a very large increase (about 45%) since the 1930's, the extremists have only augmented their lists by about 4½% (only one-tenth as much). This would seem to suggest, on the one hand, that the tendency to *increase* the number of hexapod families is becoming less, but that, on the other, the tendency to *recognize* more families is becoming greater. It may perhaps be inferred, therefore, that the situation is gradually approaching stability, and I would venture to suggest that the maximum number of families is unlikely greatly to exceed one thousand.[5] In the only recent work in which the efforts of numerous specialists have been pooled (Grassé, 1949-1951) the number of families is well below the maximum, although considerably above that of the conservatives. Some of the specialists are "lumpers" and some are "splitters," as indicated on the one hand by the treatment of the Coleoptera (especially the Caraboidea) and Orthoptera (particularly the Ensifera), and on the other by the Lepidoptera and Hemiptera—see Table 3.

Table 3 also indicates the way in which families have been distributed among the bigger orders. A largely recent rise in the number of families in each order is apparent, but it is evident that there is a greater increase in certain groups (e.g., the Hemiptera and orthopteroids) than in others (such as the Lepidoptera and Hymenoptera). This probably reflects the more intensive and sustained study that the latter have received over a longer period as compared with the former. Almost the same pattern is followed in these large orders individually as has been al-

[5] The figure of 942 given by Brues et al. (1954) is not maximal. In the Orthoptera, s.str., for instance, the authors do not list all families, although in the Blattodea they give more than are recognized by most workers. However, Princis (1960) has just proposed a system for the Blattodea recognizing even more families than Brues et al. (see Table 4).

TABLE 3—NUMBER OF FAMILIES OF LIVING HEXAPODA DISTRIBUTED IN THE MAJOR ORDERS, ACCORDING TO VARIOUS AUTHORS.

AUTHOR	ORTHOPTERA (SENS. LAT.)	HEMIPTERA	COLEOPTERA	LEPIDOPTERA	DIPTERA	HYMENOPTERA
Westwood (1839)	6	19[2]	73	21	24	19
Kirby (1885)	6[1]	26[3]	73	100+[4]	38[5]	26
Sharp (1895–1899)	6[1]	34[3]	86	53	43	23
Berlese (1920)	6[1]	22[3]	27[6]	26	28[5]	14
Handlirsch (1925)	19	45[3]	97	39	40	24
Imms (1925)	7	34+	96	57+	49	72
Comstock (1925)	7[1]	44[3]	109	70	75	49
Tillyard (1926)	9	47	74	66	50	68
Handlirsch et al. (1926–1938)	26	57[3]	109	102	121	42
Brues and Melander (1932)	43	110	176	143	125	107
Imms (1934)	7	41	95	80	47	78
Lameere (1934–1938)	14?	40[3]	73[6]	58	56	26+
Comstock (1940)	7[1]	44[3]	109	70	75	49
Grassé (Ed.) (1949–1951)	72	79[3]	187	85	121	92
Grandi (1951)	33	48	76	63	75	42
Brues et al. (1954)	50	120[3]	182	118	136	109
Imms et al. (1957)	21	95	133	89	84	78

[1] Blattodea, Mantodea, Grylloblattodea, Phasmatodea, and Saltatoria only.
[2] Including Homoptera; these authors regard Heteroptera and Homoptera as separate orders.
[3] Excluding Siphunculata, included by these authors.
[4] High count is a reflection of 19th century ardor of amateur lepidopterists.
[5] Excluding Suctoria, included by these authors.
[6] Excluding Strepsiptera, included by these authors.

ready described for the hexapods as a whole. Two schools of thought are evident: the extremists—who recognized a large number of families early on, the number of additional families recently recognized being comparatively small (see, for example, the Coleoptera)—and the conservatives—who currently recognize a larger percentage increase in the number of families.

The situation in respect of the orthopteroids is further analyzed in Table 4 to show the distribution of families within the different orders constituting the old order Orthoptera, sensu lato. The most obvious feature is the wide difference of opinion which has existed for a long time, not only in respect of ordinal status but also regarding the number of families in each group. For example, Brues and Melander (1932) recognize considerably more families of cockroaches

TABLE 4—NUMBER OF FAMILIES OF LIVING INSECTS BELONGING TO THE OLD ORDER ORTHOPTERA, AND THEIR DISTRIBUTION AMONG ORDERS CURRENTLY RECOGNIZED (ACCORDING TO VARIOUS AUTHORS).

AUTHOR	ORTHOPTERA (SENS. LAT.)	DICTYOPTERA (BLATTODEA + MANTODEA)	BLATTODEA	MANTODEA	GRYLLOBLATTODEA	PHASMATODEA	ORTHOPTERA (SENS. STR.)	TOTAL
Westwood (1839) Kirby (1885) Sharp (1895–1899) Berlese (1920)	6[1]	—	(1)	(1)	—	(1)	(3)	6
Imms (1925)	7	—	(1)	(1)	(1)	(1)	(3)	7
Comstock (1925)	7[2]							
Handlirsch (1925)	—	—	1	1	(1)	5	12[3]	19
Tillyard (1926)	9	—	(1)	(1)	(1)	(1)	(5)	19
Handlirsch (1929–1930)	—	—	7	2	(1)	3	14[3]	26
Brues and Melander (1932)	—	—	24	1	1	5	12	43
Weber (1933)	—	—	4+	2	(1)	3	12[3]	21+
Imms (1934)	7	—	(1)	(1)	(1)	(1)	(3)	7
Lameere (1934–1938)	—	3?[3]	(1?)	(1?)	(1)	2	9	14?
Weber (1938)	—	—	4+	1?	(1)	3	11+[3]	19+
Comstock (1940)	7	—	(1)	(1)	(1)	(1)	(3)	7
Essig (1942)	—	—	3	1	1	3	7+	15+
Chopard[4] *in* Grassé (1949)	—	23	(10)	(13)	1	7	41[5]	72
Grandi (1951)	—	—	7	1	1	7	17	33
Borror and Delong (1954)	11+	—	(1)	(1)	(1)	(1)	(7+)	11+
Brues et al. (1954)	25[6]	—	25	(1)	(1)	(6)	(17)	50
Ross (1956)	—	3[7]	(1)	(1)	(1)	(1)	7+[8]	10+
Imms et al. (1957)	—	2	(1)	(1)	1	3	15	21
Maximum current	—	36?	(28)[6]	(8?)	1	2	47[5]	86?

Figures in parentheses are for groups recognized below ordinal level. A plus sign indicates all families not listed.

[1] Excluding Dermaptera and other groups now removed from the orthopteroids.
[2] Excluding Hemimeridae.
[3] Including Grylloblattidae.
[4] The only author who is a specialist in the group.
[5] High number mainly due to recent elevation of certain subfamilies of Tettigoniidae, Gryllidae, and Acrididae and the recent erection of some new families.
[6] Excluding Blattodea.
[7] As "Cursoria," includes Phasmatodea.
[8] Princis (1960).

than of all other "Orthoptera" together. Even with an increase in these other groups, Brues et al. (1954) still recognize as many cockroach families as they do of the other groups combined, whereas Chopard (*in* Grassé, 1949), by contrast, indicates less than half as many families of Blattodea constituting only one-seventh of his total number of orthopteroid families. It may be noted also that the trend to increase the number of saltatorian families has continued, whereas most of the recent work on cockroaches, mantids, and phasmids has brought about a decline in the maximum number recognized (see, however, footnote 5). It is also interesting to note that although about 86 families of orthopteroids are currently recognized by some specialists—and this number may perhaps be excessive (especially for the Blattodea and Ensifera)—Sharp (1895) listed no fewer than 61 subfamilies, although these were admittedly somewhat differently disposed among the various groups.

In summary then, there is undoubtedly a tendency to increase the number of hexapod families, and, of all the orders, it is probably the Orthoptera, sensu stricto, of which it may most truly be said that this tendency is current—meaning also 'recent.'

Some Reasons for Increased Recognition of Orders and Families

It has been established that there is indeed a current tendency to erect more families, and it is also suggested that more orders are being generally recognized than formerly, even if new orders are not being proposed. Why should this be? Is it because there is a feeling that more 'pigeon-holes' are needed to accommodate more species, or are we attempting to do something else? Do we not all deduce from our classificatory system something regarding interrelationships between groups in accordance with their rank? When the Ephemeroptera, Odonata, Neuroptera, Mecoptera, and the rest were all lumped together, entomologists thought of them as one group, and yet we now know and accept that they are nothing of the kind. Even today there is still a tendency to throw the Dermaptera in with the orthopteroids. Such a procedure blurs our thinking and the recognition of more orders is one way of counteracting this.

As we constantly discover more and more species, we also come to learn more about those species we already know. There is a gradual accumulation of knowledge and we often find that resemblances between different forms are merely superficial and that, in reality, great rifts exist between previously associated groups (as in the examples mentioned). This is a continuing process; the more we learn, the more differences (or similarities) we discover, and the number of taxa that we recognize is constantly varying, in most cases increasing, to comply with our discoveries. But as our knowledge of the different groups becomes more complete, the number of *additional* groups that we recognize becomes less.

Another reason for recognizing more families and orders of living insects undoubtedly derives from our increasing knowledge of fossil forms. Indeed the basis of the most modern systems of insect classification stems from studies of fossils such as those of Handlirsch (1908) and Martynov (1938). The realization that almost all the recent major groups have existed as distinct entities for aeons gives added weight to arguments in favor of recognizing more rather than fewer orders. One must go back a very long way into the past to discover links between modern orders, even where such links can be found. The Dictyoptera and the Saltatoria, for example, have been more sharply differentiated for a longer period than have the universally recognized vertebrate *classes* Reptilia and Mammalia, so that, on a comparative basis, there really should be no argument about their separate ordinal status.[6]

[6] The two groups are easily distinguishable as far back as the Upper Carboniferous.

A further reason sometimes given for recognizing more taxonomic units—and one which in my opinion is unsound—is that entomologists tend to be overwhelmed by the enormity of the number of species with which they must deal. With probably in excess of a million species to cope with, the insect taxonomist may often feel justified in recognizing more families merely to make his task of identification less onerous. Ichthyologists (or some of them) have carried this idea to the extreme. With a mere 40,000 species to contend with, they recognize some 600 families; a thousand families of hexapods, therefore, would not seem excessive—even allowing for the fact that no uniform pattern is adhered to in nature.

In actual fact, however, there is less tendency to subdivide the orders containing the largest number of species and it is more among the 'minority groups' that additional families are being recognized. There is no tendency to break up that largest of all orders, the Coleoptera, into smaller orders (in fact there is an opposite trend to add to them the Strepsiptera); the tendency is not to preserve the Homoptera and Heteroptera as separate orders, but to reunite them. It is in fact the small group Megaloptera which is being separated from the not very large Neuroptera, or the minute order Zeugloptera which is being taken away from the Lepidoptera, leaving this great order virtually unchanged in size. Even the break-up of the Orthoptera, sensu lato, a fairly large group, cannot be attributed to this cause, for it is not one of the giants and even the largest "break-away" order, the Dictyoptera, constitutes a distinct minority.

Another common practice—as for example among the ichthyologists and ornithologists—is to create new families by elevating subfamilies to family status, all the subsidiary categories thus being, as it were, raised one rung on the ladder, permitting the erection of more taxa at the bottom. This is an insidious practice, exactly following "Parkinson's Law" which may be paraphrased: "the number of taxa expands to fill the vacancies available for their reception." There is no good reason why, if for some reason, it is desirable to raise a subfamily to family status, it should automatically be split up into further subfamilies. The grasshopper family Pyrgomorphidae is a case in point; it includes no subfamilies. Similarly, there is no good reason why an order should not consist of a single family (even a large one) if it is sufficiently homogeneous, but some entomologists are perhaps guilty of the type of "splitting" referred to. Brues and Melander (1932), or the authors whom they followed, would appear to have adopted this procedure in some cases (e.g., with the Blattodea), although not with others. The Orthoptera-Ensifera may perhaps be regarded as having received somewhat similar treatment by Chopard (*in* Grassé, 1949). On the other hand, Dirsh (1956) in the Orthoptera-Caelifera raised several minority groups of Acridoidea to family status without elevating the larger subfamilies and without making subfamilies out of previously existing tribes in his new families (see Table 5).

Recognition of Orders and Families

So far we have discussed the question of increasing numbers of higher taxa on a more or less factual basis. We should now give some attention to the desirability, or otherwise, of such trends by considering the basis on which we recognize families or orders.

It has been pointed out by Blackwelder (1959) and others that specialists may become engrossed in the structure of their own particular groups and lose sight of that of others, so that such groups become elevated to higher and higher levels in the hierarchy without reference to conditions in other groups. Should we therefore follow the specialists who *ought to* be in a better position to clarify the situation, or should we sit in judgment upon

TABLE 5—FAMILIES AND SUBFAMILIES OF ACRIDOIDEA ACCORDING TO CHOPARD AND DIRSH. (Groups marked with an asterisk are fairly generally recognized with the status indicated.)

CHOPARD (*IN* GRASSÉ 1949)		DIRSH (1956)	
FAMILY	SUBFAMILY	FAMILY	SUBFAMILY
Tetrigidae*	—	[Tetrigidae* [1]]	—
Eumastacidae*	(not listed)	Eumastacidae* (after Rehn)	Gomphomastacinae*
			Biroellinae
			Morabinae
			Choreotypinae*
			Eruciinae
			Euschmidtiinae
			10 others not studied
—	—	Tanaocer[ot]idae	—
Pneumoridae*	—	Pneumoridae*	—
—	—	Xyronotidae	—
—	—	Trigonopterygidae	—
Proscopiidae*	—	Proscopiidae*	—
—	—	Charilaidae [=Pamphagodidae]	—
Pamphagidae	Pamphaginae*	Pamphagidae	—
	Batrachotetriginae* [2]		—
Pyrgomorphidae	Pyrgomorphinae*	Pyrgomorphidae	—
	Chrotogoninae [2]		—
—	—	Lentulidae	—
—	—	Lathicer[ot]idae	—
Ommexechiidae	[Ommexechiinae*]	Ommexechiidae	—
—	—	Pauliniidae	[Pauliniinae*]
Romaleidae	—	Acrididae*	Romaleinae*
Catantopidae	[Cyrtacanthacridinae*]	—	Catantopinae*
	—		Calliptamini
	—		Euryphyminae
	—		Hemiacridinae
	—		Eremogryllinae
	—		Egnatiinae*
Acrididae*	Acridinae*	—	Acridinae* [3]
	Oedipodinae* [2]		—
			Truxalinae [2]

[1] Not studied by Dirsh; should probably be placed in a separate superfamily.
[2] Do not deserve more than tribal status (Batrachotetriginae are included in Thrinchini).
[3] Including Oedipodinae (auctt.).

them, rejecting their views when we (who know least about the matter) consider these too extreme? If we do neither of these things we become as ostriches, burying our heads in the sand; we go our own misguided ways, without reason other than subjective personal prejudice or utilitarian motives. We might in fact descend to the level of the amateur gardener who gives lip-service to the taxonomist while at the same time ignoring or failing to appreciate his achievements and continuing to use outmoded nomenclature. As Blackwelder (1959) and others have also pointed out, there are, as yet, no objective methods of assigning different taxa to their appropriate position in the hierarchy, and one inclines to the view that one should follow the specialists, who are best able to judge. There may, however, be legitimate objections to the action of some of the extremists.

Where there are many specialists in a group which has received much attention for a long time (as with the Coleoptera, for example) it seems to be more possible (even allowing for the fact that specialists never agree) to obtain a reasonable consensus of opinion regarding the status of a particular group. Thus the

general entomologist's conception tends to differ less from that of the specialist in the case of a well-known order than in that of a group which has received less attention and which has proportionately fewer specialists working with it (for example, the Orthoptera).

At present one of the criteria (if such it can be called) that is used in recognizing different groups as families or orders is the purely subjective one of familiarity. One may illustrate this by reference to the Coleoptera. The Cicindelinae are accepted by almost all entomologists as having family status: they are distinctive insects familiar to all. Crowson (1955), however, although he has indicated that this group does not really warrant separation from the Carabidae, continues to recognize it as a family as a concession to what might be termed "public opinion." Similarly the oedipodine grasshoppers (because most of them are easily distinguishable by their general facies) are still given wide recognition as a subfamily, although there is no good morphological evidence to support this. On the other hand "public opinion" is frequently against recognition of unfamiliar groups that have good claims to separate status—an example of this is the Zeugloptera. Contrariwise, many entomologists accept Homoptera and Heteroptera as distinct orders, but cheerfully place the much more divergent Saltatoria and Dictyoptera, together with other distinctive groups, in a single order Orthoptera, although they would perhaps recoil from incorporating the Isoptera (which are much closer to the cockroaches than are the grasshoppers and crickets) in the same order. If the cockroaches are Orthoptera, then so are termites; if Zeugloptera are Lepidoptera, then so are Trichoptera!

Further examples of inconsistency could be given. For instance, the Anthomyiinae are still widely given family status distinct from the Muscidae (with which they are now combined by most dipterists), but in the Acridoidea there is reluctance, even among some orthopterists, to accord family status to the Pyrgomorphidae which are much more readily distinguishable from the Acrididae than are the "anthomyiids" from other Muscidae. So far there seems to be no satisfactory objective or logical way of dealing with this problem, although Gregg (1954), drawing to some extent on the publications of J. H. Woodger, has made an attempt to apply symbolic logic to taxonomy. Philosophical discussions of this kind, however, fall more within the province of other contributors to the symposium of which this paper was a part.

Another difficulty arises when we try to interpret what it is that classification is trying to achieve. If we are trying to attain a phylogenetic system, as many believe should be our aim, we will undoubtedly use different standards for recognizing groups from what we would if we think of a classification system only in terms of practical utility. Whatever our approach, however, we must, if we cannot be objective, at least try to be less subjective.

First, we must endeavor to avoid confusing the issue, confining our attention to living forms—or at least to those which have existed since the Mesozoic. Secondly, there should be clear and fundamental morphological distinctions between the different orders or families even though it is impossible for us to insist that differences between two families or two orders should be of the same magnitude throughout the animal kingdom (or even the Hexapoda). Where differences are not fundamental or intermediate forms exist (and it is often difficult to determine if such forms are indeed intermediate in sum total of characters), we may for practical reasons be obliged to recognize suborders or subfamilies, but we should not, under these circumstances, recognize primary categories such as order and family. (The greatest difficulty comes in trying to agree as to what is a fundamental difference and what is not!)

For example, the Blattodea are clearly and distinctly separable from the Salta-

toria by numerous basic characters—even the untrained can tell the difference in every case—and their similarities are of a generalized nature. The Mantodea are likewise separable from the Saltatoria, largely by the same criteria, but although mantids are superficially very different from cockroaches they are basically very similar except in body proportions. More characters unite them than separate them, so that it is preferable to regard both as belonging to a single order Dictyoptera, but distinct from the Saltatoria. (There are of course those who would say that one never would mistake a mantid for a cockroach, therefore place them in separate orders—but the same could be said about cats and dogs.) The Grylloblattodea, however, may in some way be thought of as intermediate between the Dictyoptera and Saltatoria, which would negate this conclusion, but they are in fact quite different from both. The converse is true of the archaic Coleorrhyncha (Peloridiidae) which are sufficiently similar to both Homoptera and Heteroptera (and particularly to the former) to indicate that only one order should be recognized.

Thus the recognition of "taxonomic gaps," which undoubtedly exist at the present time, is important in establishing a higher category hierarchy. The wider the overall gap, the greater the justification (or even necessity) for separation at a higher level; the narrower the gap, the less is the justification. Whether or not these gaps extend back into the remote past is important to our understanding of phylogeny, but such considerations should not cloud our thinking in respect of classification of living organisms. Classification should be based on phylogeny, not ruled by it. Evolutionary divergence is the only good evidence we have for higher category separation—provided the divergence involves a sufficient number of "basic" characters and provided its *extent* is great enough as we see it *at the present time.*

At the family level it should also be possible to draw a reasonably clear line between one family and another. If no clear distinction exists, we should not accept more than one family. (The difficulty is to recognize the significant and fundamental differences and to avoid being taken in by evolutionary convergence or mistaking specialization for divergence.) The Acrididae, sensu lato, have several times in the past been divided into different families, and some of these, such as the Tetrigidae, Pneumoridae, and Proscopiidae, have retained their status. Other families, however, have not survived and have dropped back to the subfamily level for want of evidence that they merited full family status.

With regard to the acridoid families mentioned it may be noted that Chopard (*in* Grassé, 1949) resurrected some of these without giving reasons for doing so, but Dirsh (1956), following up investigations by Roberts (1941) and by himself, presented a classification of the group into families and subfamilies based on the phallic structures which provide fairly discrete differences between those taxa which he considers to be families, but not between others (see Table 5). There may be disagreement with Dirsh's classification, but at least there is an attempt to base conclusions on characters which are less liable to vary, and which are thus less arbitrary. His work also provides an example of a current tendency to increase the number of families for reasons other than mere elevation of subfamilies. A few subfamilies have, in fact, been so elevated (though sometimes not in their entirety), but others have not. The Oedipodinae have in fact been demoted and are no longer recognized since their former separation from the Acridinae depended solely upon superficial relative characters not applicable to all members of the group.

Conclusion

However desirable on utilitarian grounds it may be to attempt to preserve a *status quo* in the higher taxonomy of

insects, I believe enough has been said to indicate that, firstly, there never has been a *status quo* and, secondly, that as long as research continues there will continue to be changes in the number of higher taxa of all categories. As time passes, however, there will be an increasingly greater degree of stability and this will be achieved more rapidly in the case of groups, such as the Coleoptera, which, despite their numbers, have received greater attention, than in the case of such orders as the Orthoptera, which have received less.

In attempting to attain some degree of stability, it would seem that greater stress should be placed on overall differences in recognizing higher categories. The "taxonomic gaps" which are often tacitly recognized should be stressed by elevating the groups concerned to their appropriate level in the hierarchy. Conversely where gaps are insufficiently apparent, this fact should be pointed out more forcibly by amalgamation of insufficiently distinctive groups at the appropriate level.

"In the future we can expect little change in classification, only refinement as it becomes based more and more upon the total properties of the taxa and less and less upon so-called taxonomic or key characters. . . . Classification must be expanded to take into account all of the properties of the taxa" (Wharton, 1959).

Summary

1. There is apparently no current tendency to increase the number of living orders of hexapods, although there is a tendency among entomologists in general to *recognize* more.

2. There is a distinct tendency for the number of families of living hexapods to be increased, but it is suggested that, although the number of families generally recognized is constantly increasing, the tendency toward absolute increase in numbers is becoming less. A more stable situation is gradually being approached. It does not seem probable that many more than 1000 families of hexapods will be recognized in the foreseeable future.

3. The need for a more objective approach to the problem of status among higher taxa is required. It is probably impossible to equate the status of one group of animals to that of animals in other groups, but at the ordinal and family levels there should be, so far as possible, clear-cut means of differentiating one group from another—at least so far as living forms are concerned. If "taxonomic gaps" exist they should be recognized by elevating the group concerned to the appropriate category or *vice versa*.

4. Controversies will continue, but as research proceeds these will become less. We should incline toward accepting the views of specialists rather than adhering to outmoded systems.

5. It is of relatively little importance whether a group be placed at one level in the hierarchy or another, so long as the group is reasonably homogeneous and is approximately equated with comparable related groups.

REFERENCES

BERLESE, A. 1920. Classificazione degli insetti. *In* Gli Insetti; loro organizzazione, sviluppo, abitudini e rapporti coll'uomo. Società Editrice Libraria, Milan, 2:189–206.

BLACKWELDER, R. E. 1959. The functions and limitations of classification. Syst. Zool., 8:202–211.

BÖRNER, C. 1904. Zur Systematik der Hexapoden. Zool. Anz., 27:511–533.

BORROR, D. J., and D. M. DELONG. 1954. An introduction to the study of insects. Rinehart, New York, 1030 pp.

BRAUER, F. 1885. Systematische-zoologische Studien. Sitzungsber. Akad. Wissensch. Wien, Math. Naturwiss. Kl., 91, Abt. I: 237–413.

BRUES, C. T., and A. L. MELANDER. 1932. Classification of insects. A key to the known families of insects and other terrestrial arthropods. Bull. Mus. Comp. Zool. Harvard, 73:1–672.

BRUES, C. T., A. L. MELANDER, and F. M. CARPENTER. 1954. Classification of insects. 2nd ed. Bull. Mus. Comp. Zool. Harvard, 108, 917 pp.

CHAPMAN, T. A. 1917. *Micropteryx* entitled to ordinal rank: order Zeugloptera. Trans. Entomol. Soc. London, for 1916: 310–314.

COMSTOCK, J. H. 1925. An introduction to entomology. Comstock Publishing Co., Ithaca, New York, 1044 pp.
1940. An introduction to entomology. 9th ed. Comstock Publishing Co., Ithaca, New York, 1064 pp.
COMSTOCK, J. H., and A. B. COMSTOCK. 1906. A manual for the study of insects. 6th ed. Comstock Publishing Co., Ithaca, New York, 701 pp.
CROWSON, R. A. 1955. The natural classification of the families of Coleoptera. Nathaniel Lloyd and Co., London, 187 pp.
DIRSH, V. M. 1956. The phallic complex in Acridoidea (Orthoptera) in relation to taxonomy. Trans. Roy. Entomol. Soc. London, 106:223–356.
ESSIG, E. O. 1942. College entomology. Macmillan Co., New York, 900 pp. Reprinted 1954.
GRANDI, G. 1951. Introduzione allo studio della entomologia. Edizioni Agricole, Bologna, 2 vols., 950 and 1332 pp.
GRASSÉ, P. P. (ed.). 1949, 1951. Insectes. Traité de Zoologie. Mason and Cie., Paris, vol. 9, 1117 pp.; vol. 10, 1948 pp.
GREGG, J. R. 1954. The language of taxonomy: an application of symbolic logic to the study of classificatory systems. Columbia University Press, New York, 71 pp.
HANDLIRSCH, A. 1908. Die fossilen Insekten und die Phylogenie der rezenten Formen. Verlag Wilhelm Engelmann, Leipzig, 1430 pp.
1925. Systematische Übersicht. *In* C. SCHRÖDER (ed.), Handbuch der Entomologie, Jena, vol. 3:377–1143.
HANDLIRSCH, A., J. MEIXNER, M. BEIER, H. ZERNY, and F. HENDEL. 1926–1938. Insecta =Insecten. *In* W. KÜKENTHAL, and T. KRUMBACH (eds.), Handbuch der Zoologie, vol. 4:403–2490.
HINTON, H. E. 1946. On the homology and nomenclature of the setae of lepidopterous larvae, with some notes on the phylogeny of the Lepidoptera. Trans. Roy. Entomol. Soc. London, 97:1–37.
IMMS, A. D. 1925. A general textbook of entomology, including the anatomy, physiology, development and classification of insects. Methuen and Co., London, 698 pp.
1934. A general textbook of entomology. 3rd ed., 727 pp.
IMMS, A. D., O. W. RICHARDS, and G. G. DAVIES. 1957. A general textbook of entomology. 9th ed., 886 pp.
KIRBY, W. F. 1885. Elementary textbook of entomology. London, 240 pp.
LAMEERE, A. 1934. Les caractères fondamentaux des insectes. Les insectes inférieurs. Précis de zoologie, Liège, 4:57–468.
1938. Les insectes supérieures, Stégoptères, Diptères, Lepidoptères, Coleoptères, Hymenoptères. Précis de zoologie, Liége, 5:1–536.
LATREILLE, P. A. 1831. Cours d'entomologie ou de l'histoire naturelle des Crustacées, des Arachnides, des Myriapodes, et des Insectes, a l'usage des élèves de l'école des museum d'histoire naturelle. Librarie de Roret, Paris, 1, 568 pp.
LINNÉ, C. VON. 1766–1767. Systema Naturae. 12th ed., vol. 1:1–532; vol. 2:533–1327.
MARTYNOV, A. V. 1938. Études sur l'histoire géologique et de phylogénie des ordres des insectes (Pterygota, 1ª partie: Paleoptera et Neoptera-Polyneoptera. Trav. Inst. Paléont. Acad. Sci. URSS, 7 (no. 4), 150 pp.
MAXWELL-LEFROY, H. 1923. Manual of entomology; with special reference to economic entomology. Edward Arnold and Co., London, 541 pp.
PACKARD, A. S. 1882. Guide to the study of insects. 7th ed. Henry Holt and Co., New York, 715 pp.
PRINCIS, K. 1960. Zur Systematik der Blattarien. Eos, Madrid, 36:427–449.
ROBERTS, H. R. 1941. A comparative study of the subfamilies of Acrididae (Orthoptera) primarily on the basis of their phallic structures. Proc. Acad. Natur. Sci. Philadelphia, 93:201–246.
ROSS, E. S. 1956. A textbook of entomology. 2nd ed. John Wiley and Sons, New York, 519 pp.
SHARP, D. 1895, 1899a. Insecta. Cambridge Natural History. Macmillan Co., London, vol. 5:81–584; vol. 6, 626 pp.
1899b. Some points in the classification of the Insecta Hexapoda. Proc. Congr. Internation. Zool., 4:246–249.
SHIPLEY, A. E. 1904. The orders of insects. Zool. Anz., 27:259–262.
TILLYARD, R. J. 1926. The insects of Australia and New Zealand. Angus and Robertson, Sydney, 560 pp.
WEBER, W. 1933. Lehrbuch der Entomologie. Verlag Gustav Fischer, Jena, 726 pp.
1938. Grundriss der Insektenkunde. Verlag Gustav Fischer, Jena, 258 pp.
WESTWOOD, J. O. 1839, 1840. An introduction to the modern classification of insects; founded on the natural habits and corresponding organization of the different families. London, vol. 1, 462 pp.; vol. 2, 746 pp.
WHARTON, G. W. 1959. The future of systematic zoology. Syst. Zool., 8:82–87.

D. KEITH McE. KEVAN is Professor of Entomology at Macdonald College, McGill University, Quebec, Canada.

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Manuscripts must be mailed flat, not folded or rolled. They must be typed double-spaced on standard typewriter paper, with ample margins on all four sides. Double-spacing applies to all parts of the manuscript—footnotes, legends of figures, literature list, tables, etc. Footnotes are numbered consecutively and may be placed in the text between horizontal lines or listed on a separate page. Literature list will be headed REFERENCES and will follow style in recent issues of the journal, thus: name of author, year, exact title, journal name abbreviated, volume number, first and last pages. Journal abbreviations may follow usage in *Biological Abstracts*. Avoid excessive abbreviation as in the *World List*, not recommended. Journal names consisting of a single word (*Science, Evolution, Genetics*, etc.) are written out in full, as are also names of unusual or rare journals. Geographic names (*London, California*) are not abbreviated. Number of issue of a journal is not wanted unless such issues are repaged. Number of figures and plates may be omitted. Books are referred to as follows: author, year, exact title, name of publisher, location of publisher. Tables are typed on separate sheets placed in correct sequence in the text. Tables are expensive to set and should be limited to the strictly necessary. Avoid vertical lines. Illustrations should preferably be prepared for reproduction as line cuts, but illustrations requiring half-tone reproduction are acceptable. Illustrations are usually made larger than, but not more than twice as large as, their eventual size in the published journal. In preparing illustrations, the dimensions of the printed page (8 x 5½ inches) should be kept in mind. Figure legends are typed on a separate page placed at the end of the manuscript. The full scientific name of an animal, including the author and year, must be given the first time the animal is mentioned.

Authors receive galley proof accompanied by a reprint order and are reminded that changes in proof are expensive. They should not attempt to rewrite the article on the galley proof. The cost of alterations made in proof will be charged to the author if it exceeds ten per cent of the cost of composition. Authors should inform the editor whether or not they wish the original illustrations returned. To avoid delay authors with articles in press should keep the editor informed of any permanent or temporary change in address.